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# ECOLOGY

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## ALL FORMS OF LIFE IN RELATION TO ENVIRONMENT

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# ECOLOGY

## MEASUREMENT OF RUN–OFF AND SOIL EROSION BY A SINGLE INVESTIGATOR *

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That run-off water and soil erosion have become problems of both local and national importance is widely recognized. In fact soil erosion over at least half of the United States has reached the proportions of a national menace. To study quantitatively the amount of run-off and erosion from different topographical areas and types of soil under various climates as well as the quantities of soil lost under different methods of cropping, terracing, etc., the government has established Federal erosion stations. These are located in various widely separated areas. The accumulated results obtained at these stations are now finding an important place in the literature. Similar studies by certain agricultural experiment stations are also of great value. Results obtained by Duley and Miller ('23) in Missouri over a period of several years are indicative of the effect of herbaceous cover on run-off and erosion. The U. S. Forest Service has made similar extensive and commendable studies in relation to grazing. For example, a study of surface run-off and erosion in relation to overgrazing has been carried on for a long period of years on the Manti National Forest, in Utah (Sampson and Weyl, '18; Forsling, '31). Bates and Zeasman ('30), using erosion traps in Wisconsin, made a study of run-off rates under different conditions of forest, pasture, and cultivated fields.[1]

### NEED OF INDIVIDUAL EXPERIMENTATION

Practically all of these investigations, except those in relation to grazing, deal only incidentally with native vegetation and are concerned primarily with crops and systems of cropping. Therefore they afford little aid to the stu-

* Contribution from the Department of Botany, University of Nebraska, No. 88.

[1] It was from their work that the idea for the apparatus described in this paper was obtained.

dent of natural vegetation in studies concerning water relations. Moreover, results obtained from a particular soil type under a given set of climatic conditions will not apply except in a very general way to other soils and climates. Hence, in studying the water relations of various types of natural vegetation, there is a need of determining run-off and any consequent erosion directly in each type.

Water content of soil is not only a factor affecting plants and vegetation directly but one of the most important factors. This is true not only where water is deficient but also where it is in excess, as a result of the concomitant factor of decreased aeration. In the rougher portions of the mixed prairie, for example, the higher lands may support a nearly pure growth of *Bouteloua gracilis* and *Bulbilis dactyloides* and the lower midslopes *Andropogon scoparius*. But in ravines where the natural rainfall is supplemented by run-in water, *Andropogon furcatus* or *Panicum virgatum* may flourish. In fact, the run-off from higher ground may even furnish conditions suitable for the growth of *Typha latifolia, Scirpus validus* and other hydrophytes. Although one may obtain the actual water content from week to week by soil sampling, a clear picture of the quantitative distribution of water over the surface of the soil—the movement from higher lands to the lowlands—can be had only by actually measuring run-off. In many areas differences in vegetation can be accounted for only upon the basis of such movement. Frequently it occurs in places and amounts quite unexpected. In semi-arid and arid climates only small amounts of such water movement may exert a profound effect upon the type of vegetation. Hence a complete study of the water relations should include measurement of run-off as well as water accumulation or run-in from surrounding areas. The catch basin or interceptometer may be used for both of these purposes. It has the distinct advantages that it can be installed and operated by a single investigator along with other ecological apparatus (which should include a rain gauge), and that it is permanent and inexpensive.

## THE INTERCEPTOMETER

This type of interceptometer consists of a box of no. 22 galvanized iron 3 feet long, 8 inches wide, and 18 inches deep. It is well braced inside and furnished with a hinged, sloping top, open in front, as shown in figure 1. The cost of the box, which can be made by a local tinner, is approximately eight dollars.

After selecting the station for installment, an excavation slightly larger than the interceptometer is made at right angles to the slope. This should be just long enough to receive the container, about 10 inches wide and 18.5 inches deep, with the front (upper) wall perpendicular and smooth. The front side of the interceptometer is then fitted tightly against this wall with the upper edge about 0.5 inch below the soil surface. Soil is then tightly tamped, in filling the excavation, against the entire back wall of the container, which is thus held firmly in place. During rains the water running from the back-

wardly sloping top keeps this soil wet and firm. But during long periods of dry weather it is necessary to retamp the soil to keep the front wall tightly in place.

An area 3 feet wide and 33.3 feet long is enclosed by long strips of no. 22 galvanized iron or planed inch boards 6 inches in width. These are placed on
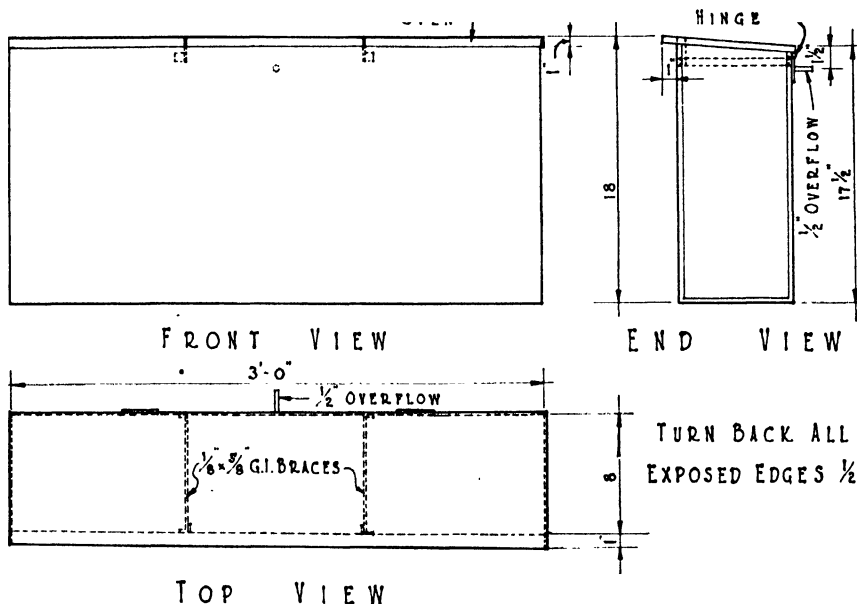


FIG. 1. Drawings showing the structure of the interceptometer.

edge in the soil to a depth of 3 to 4 inches. In the case of the boards this is best done by laying them on their side so that the outer edges include exactly 100 square feet. A shallow, narrow trench with straight walls is then dug to the proper depth, the boards placed on edge in it and held firmly by nailing to stakes securely driven into the soil just outside of the area. The trench is then filled and tamped from the outside, thus holding the framework securely in place. Thus run-in water is excluded from the experimental area.

Water running down inside the enclosed area finds its way into the interceptometer, entering under the top which is about 0.5 inch above the surface of the soil. The accumulated water should be measured and removed each day, or after every shower if desirable. In case this can be done only once each week, as at distant stations, no loss will occur if precaution has been taken to place a small quantity of oil in the interceptometer. The oil film spreading over the water prevents loss by evaporation. If the interceptometer is found to be too small to hold the run-off, a spout 0.5 inch in diameter and 2 inches long may be soldered to an opening in the back about an inch from the top. This may be connected by rubber tubing to a covered overflow container sunk

in the soil just back of the interceptometer. Where the roily or muddy water indicates soil erosion, a settling tank of appropriate size may receive the contents of the interceptometer. After settling, the clear water may be siphoned off, the sediment air dried, and thus the quantity of eroded soil determined.

An area of 100 square feet is of convenient size for comparative study of different types of grassland and the effects of clipping, grazing, or burning upon run-off. The amount of run-off and erosion from melting snow, which is often considerable, may also be measured. It is also convenient for the comparative study of grassland and various cultivated crops such as corn, wheat, alfalfa, or of fallow land. The length of the enclosure may be increased or decreased where it is desirable to determine the effect of the length of the slope on run-off and erosion (Duley and Ackerman, '34). In forested areas or those covered with scrub, larger enclosures may be more desirable in a study of the effects of thinning, cutting, burning, or denuding. The principle, however, remains the same. It is always desirable in making comparative studies of different types of natural or modified vegetation to have comparable conditions of slope and soil so far as is possible.

## ILLUSTRATIVE RESULTS

A number of interceptometers have been used during the past two years. Although the precipitation has been unusually light, some illuminating results have been obtained. One interceptometer was installed in prairie on a hillside of Lancaster loam with a slope of 10° and another 30 feet distant on a similar slope in a pasture (cf. Weaver, et al, '35). The climax prairie of little bluestem had been mowed annually; the pastured area was similar only that it had been closely grazed for a period of two years and also during the period of the experiment. Not only was the vegetation removed close to the soil but the soil itself was trampled.

A torrential April shower of .47 inch resulted in heavy run-off. This amounted to 15 liters in the prairie and 46 liters in the pasture (table I). Heavier rains on July 7 and 8, but falling over a period of several hours, resulted in 4.6 and 8.5 times as much run-off in the pasture as in the prairie where it was 1 liter in both cases. Showers of equal amounts but of different intensities on June 8 and 14 resulted in considerable differences in run-off and showed that under certain conditions practically all of the water may be absorbed even on a 10° slope.

On August 31, .25 inch and .32 inch of rain fell, each during one hour in a rain storm totaling .82 inch. Run-off was high. A day later, .47 inch of a .51 inch rain fell in an hour. It resulted in slightly less run-off in the pasture and less than half as much in the prairie (table I). During an .84 inch rain, two days later when .4 inch fell during a single hour, the pasture lost 19.9 liters but the prairie only 1.6.

TABLE I.  *Run-off from pasture and prairie*

|  | Date | Rainfall, inches | Run-off, liters | |
|---|---|---|---|---|
|  |  |  | Pasture | Prairie |
| April | 29, 1933 | .47 | 46.0 | 15.0 |
| July | 7, " | .65 | 4.6 | 1.0 |
| July | 8, " | .54 | 8.5 | 1.0 |
| June | 8, 1934 | .64 | 7.0 | 4.0 |
| June | 14, " | .64 | 1.8 | 1.3 |
| June | 17, " | .27 | 0.0 | 0.0 |
| June | 22, " | .57 | 1.7 | 0.8 |
| Aug. | 31, " | .82 | 14.5 | 8.3 |
| Sept. | 1, " | .51 | 13.7 | 2.9 |
| Sept. | 3, " | .84 | 19.9 | 1.6 |

A second installation was made for the purpose of comparing run-off in a virgin prairie of little bluestem and in an adjoining area that had been broken and cropped for a period of 6 years. The crop of winter wheat was removed from a part of the field by hoeing. This is designated as fallow field. In all cases the slope was 5°. Readings were made only when the soil was unfrozen.

On December 2, when the crop of winter wheat stabilized the dry, loose field soil, the run-off from a 1.3 inch rain was less than that in the mowed prairie (table II). A rainfall of 1.47 inches, on December 3, after the surface soil had been thoroughly wet, resulted in more than twice as much run-off in the field of wheat as in the native grassland. When the soil was again very dry (June 8), the small run-off in the prairie exceeded that in the field during a .58 inch rain. But on June 14 a rain of .87 inch resulted in greater water loss from both the field and fallow land.

The relatively heavy rains of August 31 and September 1 resulted in high run-off except in the prairie. The amount lost from the fallow land greatly exceeded that lost from the wheat stubble (table II). During the inch of rain on September 3, practically all of the water was absorbed in the prairie, 37 liters ran off from the stubble field, and twice this amount from the fallow land. Losses by erosion from these rains in the two field plots aggregated 1.5 and 5.5 kilograms, respectively.

TABLE II.  *Run-off from prairie, wheat field, and fallow land.*

|  | Date | Rainfall, inches | Prairie | Run-off, liters | |
|---|---|---|---|---|---|
|  |  |  |  | Wheat field | Fallow land |
| Dec. | 2, 1933 | 1.30 | 6.2 | 2.4 | — |
| Dec. | 3, " | 1.47 | 8.8 | 18.2 | — |
| Feb. | 24, 1934 | .28 | 0.9 | 2.7 | — |
| June | 8, " | .58 | 1.4 | 0.2 | 0.5 |
| June | 14, " | .87 | 0.4 | 14.5 | 2.3 |
| June | 17, " | .26 | 0.0 | 0.0 | 0.0 |
| June | 22, " | .54 | 0.0 | 0.0 | 0.5 |
| Aug. | 7, " | .80 | 1.8 | 6.4 | 24.3 |
| Aug. | 31, " | .74 | .2 | 14.0 | 32.5 |
| Sept. | 1, " | .65 | 2.8 | 74.5 | 85.6 |
| Sept. | 3, " | 1.01 | 1.0 | 37.3 | 73.5 |

## EXPERIMENTAL WATERING

Since little rain fell during the extremely dry summer of 1934, some experiments were made by adding water from sprinklers, thus imitating rain. Such experiments have numerous advantages over natural rainfall. By the cooperation of several workers, water may be applied at any desired rate and during any desired period of time. The behavior of the soil surface in relation to the intake of water may be directly observed under favorable conditions, the time when run-off or erosion begins ascertained, the relative turbidity or clearness of the water observed, and the period of run-off after cessation of watering determined.

In one experiment 7.5 inches of water were applied to the prairie soil during a period of three days and somewhat smaller amounts to wheat land and fallow field. The water was hauled in 55 gallon steel barrels and sprinkled uniformly over the 100-square-foot areas by 5 students, each watering an area of 20 square feet. The run-off water and eroded soil were removed, placed in settling tanks and the amount of erosion determined. The results are summarized in table III.

The watering on July 3 showed that the very dry surface soil of the prairie (with a water content below the hygroscopic coefficient) absorbed the three inches of water during 1.5 hours with only 1.5 per cent run-off. There was no erosion. The fallow field absorbed even better than the prairie during the first half hour, but soon the soil pores became partially blocked so that 18.1 per cent of the total water was lost together with approximately .008 of the surface inch of the air dried soil.[2] Sampling the following morning showed that the water had penetrated to an average depth of 14 inches in the prairie.[3]

The two inches of water applied on July 4 were absorbed by the prairie with only 5.5 per cent run-off and no erosion. The following morning the soil was wet to a depth of 16 inches near the upper end of the area and 21 inches near the foot. The fallow field lost 38.8 per cent of the water from the single inch applied and .005 of the surface inch of soil.

Water was applied to the wheat stubble on July 4 in the same amounts and at the same rate as in the prairie on July 3. The original water content of the first foot was quite as low as that in the grassland. It may be noted that the run-off was very much greater in the field after each inch of applied water; the total run-off for the three inches was 16.9 per cent. Moreover .004 of an inch of soil was removed from the surface of the field. The following morning the water had penetrated 11 inches at the lower end of the slope but only 7 at the upper end. This averaged 5 inches less than in the prairie.

With the application of a fourth inch of water to the stubble field on July 5, run-off was greatly increased, and 43.9 per cent of the fourth and fifth inch

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[2] Run-off in all cases includes the amount of eroded soil.

[3] The holes made by sampling with a Briggs' geotome were refilled with dry soil firmly tamped.

TABLE III.  *Run-off and erosion from prairie, fallow field, and wheat stubble.*

| Place | Time | Amt., inches | Run-off, liters | Remarks | Place | Time | Amt., inches | Run-off, liters | Remarks |
|---|---|---|---|---|---|---|---|---|---|
| Prairie | July 3 2:30–3:00 | 1 | 1.5 | Water clear. | Fallow field | July 3 4:00–4:30 | 1 | 0.7 | Bare soil just hoed 4" deep, rough. |
| " | 3:00–3:30 | 1 | 4.0 | Water clear, no erosion. | " | 4:30–5:00 | 1 | 43.2 | Water very turbid till end of watering. |
| " | 3:30–4:00 | 1 | 5.4 | Run-off ceased at end of watering. | " | 5:00–5:30 | 1 | 85.2 | Run-off ceased 5 min. after watering.  Total erosion 2,180 gr. |
| Prairie | July 4 9:15–9:45 | 1 | 7.3 | Run-off began after 15 min. | Fallow field | July 4 10:00–11:00 | 1 | 92.0 | Run-off began after 5 min.; ceased 5 min. after watering.  Eroded soil 1,471 gr. |
| " | 10:00–10:30 | 1 | 18.6 | Run-off ceased in 3 min. after watering.  Water clear. | | | | | |
| Wheat stubble | July 4 11:05–11:35 | 1 | 11.6 | Stubble 2.5 to 3" high. Few weeds. Water muddy. | Wheat stubble | July 5 8:45–9:15 | 1 | 73.5 | Water muddy, erosion 423 gr. |
| " | 11:35–12:05 | 1 | 43.5 | | " | 9:30–10:00 | 1 | 135.0 | Muddy. Channels formed. Erosion 1,137 gr. |
| " | 12:05–12:35 | 1 | 65.5 | Muddy, total erosion 1,188 gr. | Prairie | 10:25–10:55 | 1 | 9.7 | Water clear, no erosion. |

was lost in this manner. Also the additional two inches of water had re-
moved .005 of the surface inch of soil. While 5 inches of water wet the
prairie to an average depth of 18 inches, average water penetration in the
wheat field did not exceed 12 inches.





FIG. 2. (Above) Measuring the run-off on a 5-degree slope in *Andropogon scopa-
rius* prairie by the direct application of an inch of water every 30 minutes.
FIG. 3. (Below) Determining comparative run-off and erosion on a 5-degree slope
from wheat stubble and fallow land.

Soil samples showed that the field soil held 4 per cent more water in the
surface 4 inches five days after the 5 inches of water were applied than did
the prairie after a single day. But in the 4 to 12 inch layer the prairie soil
had 7 per cent more water than did the field soil. The higher water content
of the moist portion of the second foot of soil was also significantly greater
in the prairie.

The prairie soil had been so thoroughly depleted of its moisture that the 7.5 inches of water increased the water content only in the first 3 feet. Samples of dry soil taken during the experiments to depths of 3 feet at a distance of 3 inches outside of the enclosed areas showed that there was little lateral movement of the soil water.

Summarizing, the total run-off resulting from the application of 5 inches of water was 3.1 per cent in the prairie, 27.7 per cent in the stubble field, and 23.3 per cent in the fallow ground (where only 4 inches were applied.) Erosion from the prairie was practically nil, .009 inch of the surface from the stubble field and .013 of the surface inch from the fallow land had washed away.

One and one-half more inches of water added to the prairie during a period of 45 minutes on July 7 resulted in a run-off of only 20.5 liters.

Similar experiments were performed in the prairie and pastured area (table IV). A study of the results shows that in the prairie run-off began later in all cases, was smaller in amount, and ceased sooner after the total amount of water or any portion of it was applied. This resulted partly because of the greater interference to water movement afforded by the denser ungrazed vegetation, but perhaps chiefly to the greater porosity of the untrampled soil. The pasture had been grazed (or cut) so closely for three years that the weakened plants had partially lost their power of binding the soil, some of which would have been removed by torrential rains. On July 7 the total run-off for the 2-inch watering in the pasture was 11.3 per cent, but that in the prairie only 4.1 per cent. The third inch of water in the pasture gave a run-off of 30.2 per cent. On July 19 the percentages of run-off for the two inches of water added in the pasture and prairie were 8.6 and 2.1 per cent, respectively.

## VALUE OF EXPERIMENTS TO STUDENTS

A study of run-off and erosion caused by natural rainfall and their direct measurement by applying water are of much value in teaching. Students have opportunity to see these processes actually at work. They learn that they are directly connected with the amount of precipitation but especially with the manner in which it falls. The effect of the plant cover upon reducing the force with which the raindrops strike the soil may be clearly seen. Likewise, the beating of the raindrops upon the bare soil, the shifting of the soil particles and consequent closing of the pore spaces, and the compaction of the soil may be observed. This focuses attention upon soil structure. The accumulation of the excess water and its running off, frequently with the formation of little channels, becomes a reality. They will observe that in sheet erosion loss of materials is mostly from the dark surface soil which is high in organic matter and rich in plant food-materials. Attention is called to the loss of important nutrient elements, which may often be more serious than the loss by removal of crops.

TABLE IV. *Run-off from pasture and prairie.*

| Place | Time | Amt., inches | Run-off, liters | Remarks | Place | Time | Amt., inches | Run-off, liters | Remarks |
|---|---|---|---|---|---|---|---|---|---|
| Pasture | July 7 2:00–2:30 | 1 | 19.8 | Run-off began after 5 min. Finally ran from top to intake. Ceased 3 min. after watering. | Prairie | July 7 3:20–3:50 | 1 | 9.0 | Run-off began after 15 min., ceased at once after watering. |
| " | 2:35–3:05 | 1 | 33.7 | Ceased 2 min. after watering. | " | 3:55–4:25 | 1 | 10.3 | Run-off ceased 1 min. after watering. |
| " | 3:05–3:20 | 1 | 71.7 | Ceased 4 min. after watering. | | | | | |
| Pasture | July 19 9:20–9:35 | 1 | 20.3 | Run-off started at once, ceased 5 min. after watering. Water roily, ran from top to intake. | Prairie | July 19 10:20–10:35 | 1 | 6.1 | Run-off started in 9 min., ceased 2 min. after watering. |
| " | 9:45–10:15 | 1 | 20.3 | Water roily, slight erosion. | " | 10:45–11:15 | 1 | 3.7 | Water clear. |
| " | 11:20–11:27 | .5 | 19.5 | | | | | | |

The quantities of water lost during torrential rains even from small areas are impressive and naturally lead to calculations of the amounts running off from whole hillsides, the total amount of soil removed, the effects of this run-off water in forming gullies and ditches, and of the sediment finally silting up the fertile lowlands. The water is lost to ground storage; the deepening of gullies and ditches lowers the water table, which results in a constant tendency of the water in the upper layers to sink to lower levels. The habitat is gradually changed. The hard, compact, poor absorbing surface left after severe erosion is always impressive. That the water holding capacity is reduced is not difficult to understand. It may now be better realized that erosion can be held largely accountable for disastrous floods, on the one hand, and drought on the other. It is easier to comprehend that " most of the worn-out lands of the world are in their present condition because the surface soil has washed away, and not because they have been worn out by cropping " (Duley, '24).

Conversely, on· vegetated areas the effects of the bases of the plants in retarding the water movement may be seen. The retarding influence of the myriads of tiny dams and terraces, formed by the fallen leaves, stems and other debris, upon water movement may be learned. The porosity of the forest or moist grassland soil into which the water sinks is impressive. It accounts for the fact that on fully vegetated lands practically no erosion occurs except, possibly, during storms of unusual violence, and even then erosion is seldom serious. But on bared or sparsely vegetated slopes both run-off and erosion may occur after relatively light showers. It soon becomes clear that the most important factor tending to decrease erosion in non-tilled lands is the maintenance of a plant cover. Students learn that run-off without erosion may occur on land with a stabilized plant cover; that erosion usually increases with a decrease in plant cover, and is greatest from bared soil. Of first importance is the effort to reestablish and conserve the optimum cover of vegetation. The more complete the cover the more adaquate is the protection against soil erosion. Forsling ('31) has shown, for example, that " the increase in the density of vegetation from 16 to 40 per cent of a complete cover and the replacement of certain plants by others with more extensive and more fibrous root systems reduced the rainfall surface run-off 64 per cent and rainfall erosion 54 per cent." This results in the conclusion that, so far as possible, man should keep a crop on his cultivated fields at all times.

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# THE REPTILES OF A SAND DUNE AREA AND ITS SURROUND- INGS IN THE COLORADO DESERT, CALIFORNIA: A STUDY IN HABITAT PREFERENCE [1]

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In the spring of 1932 the author, desirous of continuing his investigation on ecology and adaptations of sand reptiles begun in the Sahara Desert, searched for a sand dune area fairly easily accessible from Los Angeles. Sand dunes were required, as it was expected to find only the most highly specialized sand reptiles habitually dwelling in an area of loose, shifting dune sand. The nearest area answering this description was found in the Coa- chella Valley, 130 miles from the campus of the University, and was selected for a thorough ecological investigation involving prolonged microclimatic records, studies of the flora, and the mammalian, avian, and invertebrate fauna. These are carried on by several colleagues at the University who joined the author in this research project, which has been generously sup- ported by research grants of the University. The present study only deals with the selection by the reptiles of habitats according to soil conditions, and with some topics concerning the relationship of the animal to its physical environment, such as wanderings, territory, etc., based on observations made on the numerous week-end trips that have been taken since April, 1932, up to the time of writing (May, 1934).

The region investigated is located 4 miles northwest of Indian Wells, Riverside County, at 33° 44′ N. and 116° 22′ W. in the Coachella Valley. The latter, the most northwesterly spur of the Colorado Desert, is bounded on the south and west by the Santa Rosa and San Jacinto Mountains, which culminate in Mt. San Jacinto (el. 10,085 ft.), and on the north and east by the San Bernardino and Chocolate Mountains—the base of which is paral- lelled by a series of lower desert ranges—the Little San Bernardino Mts., the Indio Hills, and others. The valley itself is about 60 miles long, extending from the Salton Sea in the southeast to the summit of San Gorgonio Pass in the northwest, but only averages about 5.7 miles in width, thus covering an area of 344 square miles. The floor óf the valley rises from 250 feet below sea level at the Salton Sea, to 2,559 feet above at Beaumont, at the summit of San Gorgonio Pass. The sand dune area is located at an elevation of 200 feet. The region offers an excellent opportunity for a study of habitat preference as related to structural adaptations, because several distinct habi-

tats are closely adjacent, but fairly sharply delimited from each other. Following is a brief description of the characteristics of the region.

The belt of high sand dunes, on which our attention was centered, is located on the north bank of the (usually dry) Whitewater Wash, which at this point averages about 150 feet in width. The dunes extend about 1 mile from northwest to southeast, and about ½ mile across. The dunes consist of fine, grayish-brown sand containing considerable quantities of biotite mica, but composed principally of quartz and feldspar. According to the mechanical analysis, the sand is classed as fine, although it also contains 21 per cent of very fine sand. The angular or subangular grains often show a frosted surface due to transportation by wind. Although the dunes appear

*Mechanical Analysis*

Sample No. 1

|  | Sample retained on each screen | |
| Standard mesh | Weight | Per cent |
| --- | --- | --- |
| 10 | 0.0 | |
| 20 | 0.0 | |
| 30 | trace | |
| 60 | 8.75 g. | 5.5 |
| 120 | 113.5 | 72.2 |
| 250 | 33.25 | 21.1 |
| — 250 | 1.25 | 0.8 |
| Total | 156.75 | 99.6 |

pale yellow if seen from a distance, their color is very much more pallid than that of another great dune area 16 miles west of Yuma, Arizona, also in the Californian Colorado Desert. There the sand is of a decidedly buff, almost reddish hue, and the sand reptiles from that locality (*Uma notata, Crotalus cerastes, Dipsosaurus dorsalis,* etc.) differ strikingly from those now under consideration by their reddish-buff color.

The dunes vary considerably in size, many of the bigger ones rising 25 feet or more above the level of the interdunal depressions. Owing to the prevailing (and often violent) northwest winds which sweep into the valley over San Gorgonio Pass and to which the dunes owe their existence, their lee sides face for the most part to the south and east. The same factor accounts for the tendency of the sand travelling southeast, to cross Whitewater Wash, which runs here in a roughly east-west direction, to form a dune on its south bank, and to travel from there farther southeast over the loamy ground soon to be described.

On the northwest and north, the area of high dunes is quite sharply set off from level or slightly undulating sandy land (fig. 1), on which the creosote bush (*Larrea tridentata* var. *glutinosa*) replaces the salt bush (*Atriplex* sp.), so common in the dunes. Towards the east, the dunes are

more gradually continuous into sandy land of billowy or hilly topography, much richer in vegetation and in vegetated hillocks of firm soil. Large thickets of mesquite (*Prosopis juliflora* var. *glandulosa*) grow increasingly common toward Indian Wells.



FIG. 1. The edge of the dune region, showing the abrupt change from high dunes to level or undulating sand with more abundant vegetation.

As mentioned above, the southern boundary of the dunes is formed by the Whitewater Wash, the floor of which consists of level loam cracked into polygonal plates, here and there covered with drifted sand. The south bank is crowned by one large dune, south of which the sand grows scarcer, covering only in places the level, loamy substratum (fig. 2). Packed, firm crust prevails south of a small wash, a tributary of Whitewater Wash. On the south bank of the latter and both sides of the small wash, grow numerous thickets of desert willow (*Chilopsis californica*) of varying sizes. The soil may be classed as very fine silty clay-loam, the clay fraction of which is responsible for solid, cracked plaques of the surface. Kocher and Harper ('28) classify it as " Indio very fine sandy loam."

*Mechanical Analysis*

| Standard mesh | Sample retained on each screen | |
|---|---|---|
| | Weight | Per cent |
| 10 | 0.0 | |
| 20 | 0.0 | |
| 30 | trace | |
| 60 | 0.5 | .3 |
| 120 | 7.25 | 4.8 |
| 250 | 34.0 | 22.6 |
| — 250 | 109.0 | 72.6 |
| Total | 150.75 | 100.3 |

In the following list of reptiles collected in the area, we have followed the arrangement in the new edition of Stejneger's and Barbour's check list ('33). Only those species are considered in detail which show an especially high degree of adaptation to a sandy environment and are, therefore, commonly found in the dunes.



FIG. 2. Desert willow (*Chilopsis californica*), the home of *Crotalus atrox,* south of Whitewater Wash on level, sandy-loamy ground.

*Coleonyx variegatus* (Baird).—Two specimens of this attractive gecko were collected at night, one on 'a large sand dune, the other in the sand hills east of the dunes. A third specimen was found in the stomach of a small sidewinder.

*Dipsosaurus dorsalis dorsalis* (Baird and Girard).—The Crested Lizard or Desert Iguana is quite common in Coachella Valley. Many specimens may be observed sitting on the tops of rocks or on ridges of soil along the highway between Palm Springs and Indio, and on flat or undulating sandy ground. On firmer soil close to the dunes the species is not rare, yet no specimen was found in the dunes. It is usually found on the small hillocks of firm soil, and when disturbed takes refuge in burrows. Mainly vegetarian, this lizard is sometimes found climbing in the creosote bush (*Larrea tridentata*) several feet above the ground, feeding on the blossoms.

*Callisaurus ventralis gabbii* Cope.—Although the Gridiron-tailed Lizard is quite common in Coachella Valley, only a few specimens were seen in the area investigated. One was observed on the sand dune crowning the north

bank of the wash; others on the billowy sand, and several on the bottom of Whitewater Wash. The habitat more typical for this form is a fairly level and coarse sandy-stony ground.

*Uma notata* Baird.—As the author has described in a previous publication (Mosauer, '32a), this lizard is the most highly specialized of North American sand lizards, excepting perhaps the footless burrowing *Anniella*. The wedge-shaped snout of *Uma* with a " countersunk " lower jaw, the thick, serrated eyelids, the scale fringes along the toes of fore and hind feet, the depressed broad general habitus, and also the velvety, finely granular scalation, all seem to be of value to an arenophile reptile (fig. 3). Hence it is



FIG. 3. Head end of *Uma notata,* showing some of the sand adaptations of this lizard. Note the countersunk lower jaw, the heavy, fringed eyelids, the enlarged, spiny scales on the shoulder and along the anterior border of the arm, and the scale fringe on the phalanges.

not surprising to find that the Ocellated Sand Lizard is the only reptile which shows a decided preference for the mighty barren dunes. Specimens can be seen at any time of the day on top of the dunes near the edges. Frequently they are found buried in the sand, only the head partly or fully exposed, and then are not discovered until they suddenly rush for safety almost from under foot. Often they are buried in loose sand, but just as often they leave behind them a small blind burrow with oval, depressed mouth, just large enough to accommodate their flattened wide bodies. During the hotter time of the· day these lizards are extremely wary. Apparently they have an especially keen eyesight and turn to flight when the intruder is still a hundred or more feet away. Thus one does not see much of them during a ramble over the dunes at midday except for their tracks (fig. 4, 5). These are seen everywhere on the top of the dunes, mostly closely paralleling the edges where the lizards seem to spend a good deal of their time. When disturbed, they dash over the edge and run or skid down the loose sand of the steep lee side into the shelter of the *Atriplex* bushes that grow at the foot of the dune, or into the burrows of Kangaroo Rats which offer welcome refuge to most reptiles. In spite of their apparently plump and rather heavy build the speed of these lizards is considerable.

In the field, it seems that there is hardly any limit to the amount of insolation and heat which *Uma* can withstand. Measurements of the temperature attained by the surface on the dune edges showed them to be as hot as 50°–60° C. (122°–140° F.) around noon in April and May. These, then, are the actual habitat temperatures during spring for this species. Yet, in



FIG. 4. A track of *Uma notata* made during slow locomotion, with direction from the left to the right. The marks of the individual toes are visible; the tail is dragged.

an experimental cage heated to a corresponding temperature, *Uma* perishes just as promptly (in less than ten minutes) as does the nocturnal Sidewinder. Apparently *Uma* escapes overheating by burrowing or by retreating into the shade of bushes.

It seems appropriate at this place, to discuss the explanations for the behavior of some Asiatic desert lizards offered by Kashkarov and Kurbatov



FIG. 5. A track of *Uma notata* made in fast running. The deeper pits are the impressions of the hind feet. In fast locomotion, the tail is lifted off the ground. Direction is from left to right.

('30). According to their theory, *Agama sanguinolenta* climbs up into bushes, approximately 2 meters above the ground where the temperature sometimes is 28° C. lower than that on the ground, in order to escape the heat of the latter. For a similar reason, *Phrynocephalus mystaceus* climbs at midday to the ridge of loose sand, and remains there standing on its feet, not touching the ground with its belly, in order to reduce its contact with the hot ground and to derive greatest benefit from the cooling wind.

These explanations do not agree with an analysis of typical lizard behavior. In order to escape the heat, desert forms either take refuge in the ever temperate climate of the ubiquitous rodent burrows, or bury themselves in the sand, or finally they may remain in the shade of bushes. There are several reasons why lizards may climb up into bushes: either they are searching for food—be it vegetable matter, as the blossoms of the shrub (see *Dipso-saurus dorsalis*), or insects attracted by the blossoms—or the species is habitually semi-arboreal, as *Uta* in our deserts.

Concerning *Phrynocephalus*, it is a well-known fact that many lizards tend to select a dominant point for a lookout, be it the top of a prominent rock, the edge of a dune, or some similar elevated spot. There are stretches along roads and highways in the Southwest, where almost every large rock is crowned by its *Sceloporus* regardless of the temperature, and nobody would assume that these lizards are up there just to escape the heat of the ground.

Lastly, the theory that *Phrynocephalus* stands on its feet, not touching the ground with its belly, because of the heat of the substratum, can be refuted by the simple observation, that lizards are more sensitive to heat on the sole of their feet and on their toes than on their belly. The author has seen numerous species of Old World lizards (mainly *Lacertidae*) and many American forms in a typical scene. They are warming themselves on a sunheated rock or artificial heater in the cage, flattening their bodies against the hot surface, but lifting off their sensitive feet in a fashion that reminds one of a piano player in action. The position assumed by *Phrynocephalus* is therefore much more likely one of attentiveness or wariness, an attitude often assumed by a variety of lizard species, but not an attempt to escape the heat of the ground.

*Uma* is less common on level or billowy sand than on the dunes, while no specimen was found on the level loam. It is interesting to note that the only high sand dune which has migrated across Whitewater Wash and crowns its southern bank, has its *Uma* population, the pioneers on an outpost.

*Uta stansburiana stejnegeri* Schmidt.—This inconspicuous little lizard is fairly common in the bushes of the loamy land south of the Whitewater Wash, on the banks of the Wash itself and its tributaries, and also occurs occasionally in the dunes. There, however, it is so definitely restricted to the cover of the shrubbery that the sandy habitat which surrounds it matters little.

*Phrynosoma m'callii* (Hallowell).—A specimen of this rare Horned Toad was captured in the sand hills just north of the dunes. It was half buried in the sand (about 10 a.m.) and would certainly have been overlooked had not the author's attention been attracted and directed to it by its tracks.

*Cnemidophorus tessellatus tessellatus* (Say).—The Whip-tailed Lizard shows in our region a decided preference for relatively firm soil, loam or clay. It was never found in the dune area proper, and occurs in the more level sandy stretches on the bush-covered hills of firm soil which form islands of

its typical habitat amidst the ocean of sand. *Cnemidophorus* is most common, however, on firm ground, *e.g.* loam. Its coloration is strikingly more somber than that of the light gray, almost white sand lizards and thus is more in keeping with the darker, brownish color of the loam.

*Coluber flagellum frenatum* (Stejneger).—Two specimens of the Red Racer were observed in the dune region, while a third was seen among the scattered boards of an abandoned homestead in the sand hills just north of the dunes. A very small specimen was found in our camp on the loamy ground south of the Wash. They were active in the forenoon; apparently this species is the most decidedly diurnal snake of the region.

*Arizona elegans occidentalis* Blanchard.—Several specimens of the Faded Snake, dead and alive, were found at night on the neighboring highway; one specimen was captured in the dunes at about 10:00 p.m. after its tracks were followed for about 200 feet. A captive specimen devoured an Ocellated Sand Lizard (*Uma notata*) and a Gridiron-tailed Lizard (*Callisaurus ventralis*).

*Pituophis catenifer deserticola* Stejneger.—The Gopher Snake is quite common in Coachella Valley. Several specimens, dead and alive, were found on the highway, quite close to the dune region; others were found under boards of the ruins of homesteads in the sand hills and at the margin of a date palm plantation in the neighborhood of the dunes. No specimens were collected in the dunes proper. The Gopher Snake seems to be largely nocturnal or crepuscular, to conclude from the number of specimens found on the road at night.

*Sonora occipitalis* (Hallowell).—This little snake, though not frequently collected before, is very common in the region investigated. It is one of the typical members of the reptile fauna of the sand dunes and shows distinct anatomical adaptations to life in a sandy environment. Its small, wedge-shaped head, continuous with the body without visible demarcation, its lower jaw counter-sunk into the frame of upper labials, is excellently fitted to cut through the sand in " sand swimming " or through slightly firmer soil in burrowing. Similarly, the highly polished scalation is useful in reducing friction to a minimum, and lateral keels on the ventral scales, similar to those existing in arboreal snakes, prevent slipping in the lateral undulatory movement on or in the sand (fig. 6).

This undulatory type of locomotion is used by *Sonora* for its travels on the surface, which are relatively short, hardly exceeding 100 feet in one night. The track is a very regular sinuous curve of great amplitude, and shows behind the oblique sections of the track small heaped-up sand walls which are highest at the points of inflexion of the curve, where the forces in locomotion are greatest. The tracks lead from one bush to the other and always end in some shrub-covered hillock where the snake seems to enter pre-existing burrows or small holes. In a cage with loose sand, *Sonora* readily slips into the sand and " swims " under the surface with great ease,

staying buried most of the time.   In the field, however, none of the hundreds of tracks observed indicated that the snake had left the surface on the open sand between bushes.
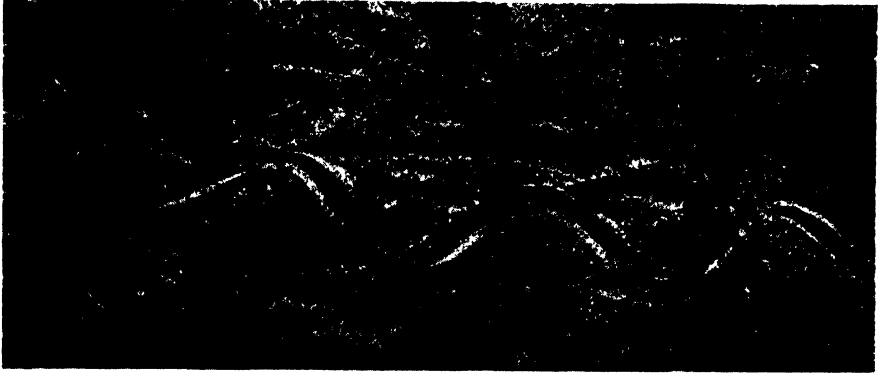


Fig. 6.   A track of *Sonora occipitalis*, typical for that of a snake using the horizontal undulatory method of locomotion.   The heavier sand piles in the rear of the oblique section indicate the direction of locomotion from right to left.

As mentioned above, *Sonora* is quite common in the dunes, and even more tracks were observed in the surrounding sand hills and on patches of loose sand on the loamy ground south of the Wash.   Because of its secretive habits, this little snake is quite elusive and is relatively rarely collected, even though as many as 11 tracks may be seen in one evening, particularly in warm weather.

*Crotalus atrox atrox* Baird and Girard.—No specimen of the large Texas Diamondback Rattler was found in the dunes proper, but numerous specimens were collected or their tracks seen in the sand hills east of the dunes, on the sandy-loamy land south of the Wash, and on or along the only dune on the south bank.   The track of one specimen was followed for a considerable distance over the dunes, down into the Wash and up the steep south side, beyond which, on sandy-loamy level ground, the specimen was found coiled under a ledge.   Although the Diamondback occasionally travels for considerable distances, it seems to be a much more " sessile " snake than the Sidewinder.   It inhabits the large thickets of mesquite and the stands of desert willow—in which I observed three specimens within a few minutes on October 23, 1932, south of the Wash—and seems to venture only little into the open.   If it does, it follows the shortest route connecting bush to bush, and crosses through every bit of vegetation on its way.   The favorite type of locomotion of the Diamondback, the caterpillar movement (fig. 7) (Mosauer, '32b, '32c, '33a) is much better suited to moving about in dense thickets through the obstructions of roots, trunks and branches, than the looping locomotion of the Sidewinder which consequently prefers " the wide

open spaces " of barren sand.  Mr. Walker, a resident of the sand hills close
to Indian Wells, who has collected hundreds of *C. atrox* close to his ranch,
and who is very well informed on the habits of the local reptiles, communi-
cated to me the following, obviously well-founded observation.  According
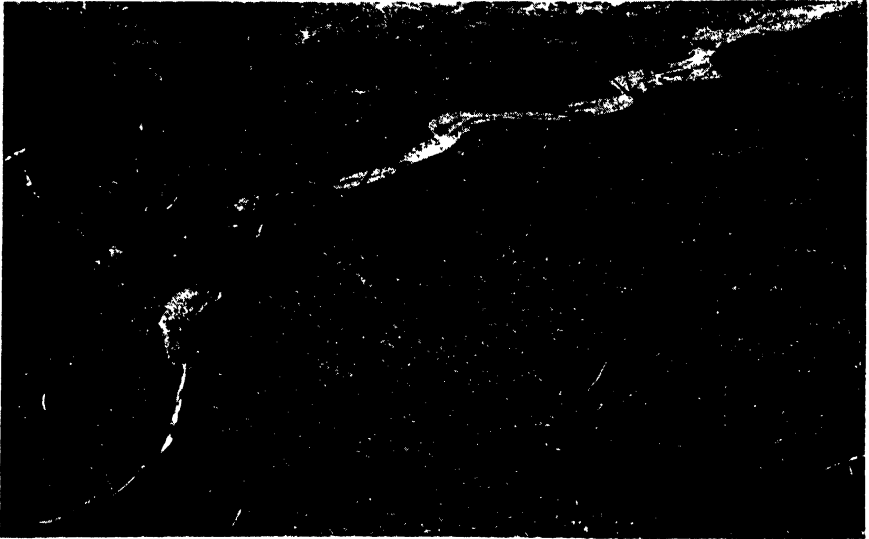


FIG. 7.  A track of the Diamondback Rattlesnake (*Crotalus atrox atrox*), typical for
a snake using the caterpillar movement.  The direction of locomotion is from lower left
to upper right, but this can not be recognized on level ground.

to him, every Diamondback has a more or less permanent refuge in a certain
thicket and travels from there over a definite route from bush to bush, fol-
lowing approximately the same route on the return, thus establishing a regular
trail which is used time and again by the same snake.  Mr. Walker tells me
that very frequently he is not able to capture a certain specimen for months,
because he never meets it out in the open, although he sees its tracks over the
same route, until he finally succeeds in overtaking the snake outside of the
dense shelter of mesquite, on its usual way to another bush.  On April 16,
1933, Mr. Walker told me of a pair of snakes which were always travelling
together, leaving parallel tracks between certain bushes.  Upon my request,
he took me to the location, and there indeed were two fresh tracks paralleling
each other, going from one mesquite bush to another.  We saw one of the
two snakes at the edge of the thicket (at 5:00 p.m. on a cool day), while
the other was apparently under shelter of the thicket.  Although this occasion
was the only one on which I was able to confirm Mr. Walker's observations,
I see no reason for doubting the veracity and correctness of his often repeated
statement.  It seems to be an interesting record of a definite territory in
snakes.

*Crotalus cerastes* Hallowell.—Although the Sidewinder, one of the characteristic animals of the dunes, shows no obvious structural adaptations to the life on sand deserts, it is nevertheless highly specialized for it in a functional manner by its peculiar type of locomotion (an anatomical peculiarity which it shares with African desert snakes of the genera *Cerastes* and *Pseudocerastes*, namely a supraocular horn above each eye, has not been explained satisfactorily). The progression from which this snake derives its name



FIG. 8. A fine track of the Sidewinder (*Crotalus cerastes*), moving from lower right to upper left. The hook at the lower right end of each track is made by the neck; the crossbar at the other end, by the tail of the snake. An insect track runs along the lower edge of the picture.

has been analyzed by the author (Mosauer, '30) as similar in principle to the sidewise rolling of a screw or helix, touching the ground only with two sections of its length (fig. 8, 9). Thereby the snake (as well as the helix) leaves a series of straight, disconnected ribbon-like impressions in the sand,

set at an oblique angle to the general direction of progression and each exactly as long as body and tail of the snake. It was mostly by means of following these typical tracks that the Sidewinders were collected and their habits studied. This was done frequently at night with the aid of flashlights



FIG. 9. Sidewinder moving towards the left of the picture.

or in the early morning, when the tracks made the night before were still fresh and unobscured, and the oblique lighting of the sun's rays sharply defined the details and outlines. It is possible to recognize the direction in which the snake was going by a hook on the rear end of each track, made by the head and neck, and by a cross mark, set at right angles to the front end of the track made by the tail (rear and front relative to the general direction of progression). The rolling locomotion is apparently well-adapted to the loose, almost fluid character of dune sand, since the speed of the Sidewinder on such substratum is considerable. In numerous speed tests conducted with freshly collected specimens in their native habitat the maximum speed was determined to be about 0.8 to 0.9 meters per second; a remarkable record in view of the fact that the Red Racer, noted for its speed, did not exceed 1.6 meters per second under analogous conditions. The locomotor efficiency of the Sidewinder is also well-demonstrated by its extensive nocturnal wanderings, which are frequently far in excess of 1000 feet. In the sand dunes west of Yuma, Arizona, tracks of a specimen were followed for 2834 feet, but this distance may not have been covered in the same night. Even very small specimens, a few days or weeks old, the tracks of which were observed in great numbers in early September, had covered distances of several hundred feet up and down over the steep dunes. The travelling habits of the Sidewinder are quite erratic; sometimes a snake proceeds for a hundred yards or more in a very " orderly " manner (in a fairly straight course) ; then again it may retrace its own track or take a zigzag or circular course. It seems to prefer the open sand to bushes, which it frequently avoids by

encircling their periphery, instead of passing through them, as *Crotalus atrox* does. In the morning, the Sidewinder is usually found coiled up in a very typical manner, its peripheral coil partly buried in the sand, in the shade of a bush, or out in the open sand. The latter position is very much rarer—in no case could Camp's observation be confirmed who found them "partly buried flush with the surface in the hot sand right out in the noonday sunshine of midsummer" (Camp, '16). It could be shown experimentally that the Sidewinder is quickly killed by overheating when exposed to the desert sunlight (Mosauer and Lazier, '33). It is active, however, in temperatures as low as 10° to 12° C. on chilly, windy nights.

The Sidewinder is quite common in the dunes and even more so on level or undulating sand, but also ventures frequently across the Wash into the level loamy territory which is partly covered by patches of loose sand.

## DISCUSSION AND SUMMARY

If we attempt to summarize the habitat relations of the reptiles of the region investigated, we find the actual field results to be in excellent agreement with the theoretical supposition that the most highly adapted sand reptiles would favor the dunes as habitat, while the less adapted forms would correspondingly prefer a less specialized environment.

*Uma notata*, the most highly modified sand reptile among North American lizards (excepting the burrowing legless *Anniella*) is the only reptile showing a decided preference for the barren festooned dunes. Its fringed toes and modified head with countersunk lower jaw render it well fitted for such an environment. Among the snakes, *Sonora occipitalis* and *Crotalus cerastes* are most highly specialized, the former anatomically and functionally adapted for burrowing as a subarenaceous form; the latter functionally adapted by its peculiar type of locomotion. Correspondingly, they are the only two species of snakes commonly found in the dunes. Yet the number of individuals is greater in the surrounding sand hills where the two chief controlling factors of distribution—character of soil and food supply—are both at their optimum.

In an investigation of the ecology of the desert reptiles of the Sahara, the author could show that desert reptiles are especially numerous in a rather narrow belt of desert around an oasis. Here they find their living conditions at their best, since they can enjoy the sandy character of the soil suitable to them and simultaneously the rich food supply afforded by migrants from the oasis. Similarly, the Sidewinder is commoner in the sand hills, although the dunes would be just as suitable so far as soil is concerned; but the Kangaroo Rats on which this snake preys are more numerous in the sand hills—hence the numerical difference in distribution of *Crotalus cerastes*. In *Sonora*, the deciding difference seems to be the existence of shrub-covered hillocks of fairly consolidated soil in the sand hills, which provide the usual habitat of

*Sonora;* in the dune area the shrubs are rarer and are restricted to the inter-dunal depressions, usually without formation of a hillock.

Besides the three permanent reptilian residents of the dunes (*Uma, Sonora, Crotalus cerastes*), there are several species which occasionally travel from their surroundings into the dune area without making their home there. We can classify such forms as migrants.

In the following table the reptiles observed or collected in the respective habitats are listed in order of their frequency of occurrence. The estimate of their relative frequency may not be altogether reliable, since the many factors involved may obscure the true picture. *Sonora,* for instance, is very secretive and elusive in its habits and the number of individuals must be judged from the numbers of tracks, not of specimens collected. On loamy ground, however, tracks are not visible, and there the probability of collecting *Sonora* is slight. *Crotalus cerastes,* on the other hand, travels extensively and leaves easily detected tracks in the sand, so that its frequency may be over-estimated. Besides, collecting was done primarily in the dunes and only incidentally in the other habitats, so that the number of specimens collected in these habitats cannot be directly compared.

TABLE I. *Reptiles collected, listed in order of frequency of occurrence* [1]

| Dunes | Level or undulating sand with richer vegetation | Level loamy ground with occasional patches of sand, south of White-water Wash, and floor and loamy bank of Wash |
|---|---|---|
| *Uma notata* (v. c.)<br>*Crotalus cerastes* (c.)<br>*Sonora occipitalis* (f. c.)<br>*Uta stansburiana elegans* (r. in bushes)<br>*Callisaurus ventralis gabbii* (r.)<br>*Coluber flagellum frenatum* (r.)<br>*Arizona elegans occidentalis* (r.)<br>*Coleonyx variegatus* (r.)<br>*Crotalus atrox atrox* (r.) | *Dipso-saurus dorsalis dorsalis* (c.)<br>*Uma notata* (c.)<br>*Sonora occipitalis* (c.)<br>*Crotalus cerastes* (c.)<br>*Callisaurus ventralis gabbii* (c.)<br>*Cnemidophorus tessellatus tessellatus* (f. c.)<br>*Uta stansburiana stejnegeri* (f. c. in bushes)<br>*Coluber flagellum frenatum* (f. c.)<br>*Crotalus atrox atrox* (f. c.)<br>*Pituophis catenifer deserticola* (f. c.)<br>*Coleonyx variegatus* (r.)<br>*Phrynosoma m'callii* (r.) | *Cnemidophorus tessellatus tessellatus* (c.)<br>*Uta stansburiana stejnegeri* (f. c.)<br>*Crotalus cerastes* (f. c.)<br>*Sonora occipitalis* (f. c.)<br>*Crotalus atrox atrox* (f. c.)<br>*Callisaurus ventralis gabbii* (f. c. in wash)<br>*Coluber flagellum frenatum* (r.) |

[1] v. c.—very common; c.—common; f. c.—fairly common; r.—rare.

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# POLLEN ANALYSIS OF SOME WATER DEPOSITED SEDIMENTS

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In the study of the paleoecology of a region it seems advisable to secure evidence from two or three separate deposits in each locality. In most localities lakes of the same age as the bog or bogs are available. It is the purpose of this paper to compare the pollen analysis of a bog with that of sediments taken from the bottoms of two lakes of the same age.

## LOCATIONS

Two lakes in northeastern Indiana thirty-eight miles apart were studied. These lakes which lie in the same glacial moraine (Wood, '15) are Center Lake, one mile northwest of Angola, Steuben County, and Smaley Lake, five miles southwest of Cromwell, Noble County. The bog used for comparison was located at the northwest end of Center lake (Houdek, '32).

## METHODS

The water-deposited sediments were collected by means of a rohrlote (fig. 1), designed and constructed by the author after Lundquist ('25). The rohrlote is essentially a large brass tube to which have been fastened four steel fins and a mass of lead the weight of the instrument being about 25 pounds. A glass tube is inserted in the lower end and held in position by a spring (fig. 2). A valve is attached to the upper end. To a handle at the top is fastened a strong rope. When dropped out of a boat, the instrument penetrates the sediments at the bottom of the lake some of which are forced into the glass tube. The valve at the top prevents the sediments from being lost when the rohrlote is being pulled to the surface, where the glass tube containing the sample is carefully removed, corked, and labeled. A number of samples were taken from each lake.

The sediments were analyzed for their pollen content by the method described by Voss ('31). The top half meter of sediment in Smaley Lake was practically devoid of pollen grains and other plant parts. It was black in color, very smooth and soft in texture, and contained many gas bubbles, all indicative of active decomposition. All the other sediments were fine textured, partially decayed peat.

The depth to which the sampling device sinks is much greater than the length of the glass tube in which the sample is secured. The sample is not as

long as the deposits are deep but represents the deposits in a compressed form. This compression is adequately discussed by Lundquist ('22). To determine the depth represented by the samples, accurate records were kept of the depth to which the rohrlote sank in the sediments. For each lake bottom two samples were analyzed and the pollen percentages combined to give one pollen diagram.



FIG. 1. The rohrlote in position for use, showing also the spring and glass tube at the right.

FIG. 2. Working drawing showing structure of the rohrlote.

## RESULTS

The pollen diagrams in figure 3 present the results of the study. The lines giving the percentages of similar pollens in the bog and two lakes are, in general, parallel. This represents a great degree of similarity in the pollen content of the three deposits. The variations between the three lines is possibly greater in one or two places than what some workers might term " expected variations," but they are not greater than variations that have been experienced in adjacent samples from the same deposit.



FIG. 3. Pollen diagrams of deposits from two lakes and one bog.
Depth in meters at the left.

## CONCLUSIONS

The bog and the two lake bottoms of the same age have presented similar pollen diagrams.

Pending further investigations, lake bottom sediments may be used to substantiate paleoecological evidence secured from bog peat.

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The pollen diagrams in figure 3 present the results of the study. The lines giving the percentages of similar pollens in the bog and two lakes are, in general, parallel. This represents a great degree of similarity in the pollen content of the three deposits. The variations between the three lines is possibly greater in one or two places than what some workers might term " expected variations," but they are not greater than variations that have been experienced in adjacent samples from the same deposit.



FIG. 3. Pollen diagrams of deposits from two lakes and one bog.
Depth in meters at the left.

## Conclusions

The bog and the two lake bottoms of the same age have presented similar pollen diagrams.

Pending further investigations, lake bottom sediments may be used to substantiate paleoecological evidence secured from bog peat.

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# THE INFLUENCE OF TEMPERATURE AND OTHER FACTORS ON THE WINTER AGGREGATIONS OF THE SUNFISH, *LEPOMIS AURITUS*, WITH CRITICAL REMARKS ON THE SOCIAL BEHAVIOR OF FISHES

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## INTRODUCTION

The factors controlling the aggregating habits of animals have received a large amount of attention from ecologists, especially in recent years, as is clearly indicated by Allee ('31), who summarized the data to that date. Strangely enough, however, the fish school—one of the most noticeable forms of animal aggregation—has received relatively scant analytical attention. Illustrative of this is the fact that Parr ('27) had virtually a clear field for his analysis of the behavior of the influences at work in a school of mackerel. Spooner ('31), who considered the schooling of a species of bass, has already noted this lack of critical literature. The significant titles dealing with these subjects are distinctly fewer than the problems involved warrant.

With these considerations in mind an experimental study of the behavior of a single species was undertaken at the New York Aquarium. In those exhibition tanks of the New York Aquarium, that are provided with running fresh water by the city mains, the seasonal influence of the temperature is distinctly evident. In the autumn, on a falling temperature, various species cease feeding when a certain threshold is reached and then suspend such activity until the warming influence of the spring is felt. Certain species incline to an extremely quiescent state, and some group themselves in closely compact aggregates. Most prominently marked in this regard are the black bass, *Micropterus dolomieu* Lacépède (especially the smaller sizes) and *Lepomis auritus* (Linnaeus). Townsend ('16) described and illustrated this condition for the black bass, noting that the aggregations formed when the temperature had dropped to about 40° F.

We wish to express our thanks to Dr. W. C. Allee for several valuable criticisms.

## EXPERIMENTAL STUDY

*Temperature.*—*Lepomis auritus* forms into a closely compacted aggregation, resting in a quiescent school when the temperature falls to 5° C. as shown in Fig. 1. At 7° C. the tendency to form such a body is only feebly present, and at 9° C. the fish swim about comparatively independent of each other and are active, but not as lively as at higher temperatures. In one

aggregation where the temperature had fallen to 4° C. warm water was slowly introduced, causing a rise in temperature to 7° in eight hours. This school did not completely break up, however, until 10° C. was reached. There may well be a temperature difference between the formation and the dissolution of a school, due to some physiological lag effect or "psychic inertia." On allowing the water to cool again, the aggregation began to re-form at 7° C. The details of this experiment together with the data are set forth in table I.

TABLE I. *Effects of Temperature on the Aggregation of Lepomis auritus (Linnaeus)*

1. Normal seasonal reduction of temperature

| Date Dec. 1933 | Temp. ° C. | Effect |
|---|---|---|
| 7 | 9 | Disperse state |
| 13 | 7 | Slight tendency to aggregate |
| Jan. 1934 | | |
| 5 | 5 | Complete aggregation |

2. Experimental modification of temperature

| Date Jan. 1934 | Temp. ° C. | Effect |
|---|---|---|
| 15 | 4.0 | Complete aggregation |
| 16 | 5.5 | Warm water introduced |
| 18 | 6.0 | Aggregation still complete |
| 18 | 7.0 | (8 hrs. later) no effect |
| 19 | 10.0 | Aggregation in slow dissolution |
| 20 | 18.0 | No aggregation. Disperse state |
| 23 | 12.0 | Still dispersed |
| 24 | 5.0 | Aggregation re-formed |
| 25 | 4.0 | Aggregation complete |

In addition to this formal experiment, casual observations in complete agreement with it have been made in the New York Aquarium by one of the present writers for three winters, and by the other for twelve. The observations of Townsend ('16) on *Micropterus,* as previously noted, at 40° F. (between 4° and 5° C.), suggest that both species have similar if not identical thresholds.

*Light.*—It has been shown that most, if not all, schooling fishes disperse at night, leading to the belief that schools are largely dependent on vision. This has been reported to be the case for *Clupea harengus* Linnaeus, by Newman ('76); for *Pneumatophorus grex* (Mitchill), by Parr ('27); for *Jenkinsia stolifera* (Jordan and Gilbert), by Breder ('29); for *Morone labrax* Linnaeus, by Spooner ('31), and for *Ameiurus melas* (Rafinesque), by Bowen ('31 and '32). Aside from these definite references it is almost certain that the same is true for many fishes, if not all schooling species.

The simple expedient used by Parr in his mackerel studies was applied to the sunfish. That is, a fish temporarily blinded with vaseline and lampblack was released in an aquarium containing a large, well condensed aggregation. This fish moved about at random for several hours after introduction. On the removal of the blindfold it immediately sought a place in the

aggregate and became part of it. This was tried several times with identical results. Furthermore, with the coming of night these aggregations would break up. This action occurred, however, in a light sufficiently strong for the observer to distinctly see the fish. The turning on of electric lights would cause the school to begin re-forming at once; the completion of this movement would require from ten to fifteen minutes. It thus becomes evident that no school is possible without enough light for the fish to see one another, and there is an integrating influence constantly at work to hold the fishes in their places. Otherwise it would be difficult to explain the rapid breaking up of a well-formed school with the turning off of the light.

*Current.*—As a current was produced in the aquarium by the inflowing water, it followed that the fish all headed into the flow, as free "floating" fishes must if they are to hold their position. This has been demonstrated by Lyon ('04, '05) and by Breder ('26). In order to detect the effect that this influence had on the actual formation of the school, the flow was
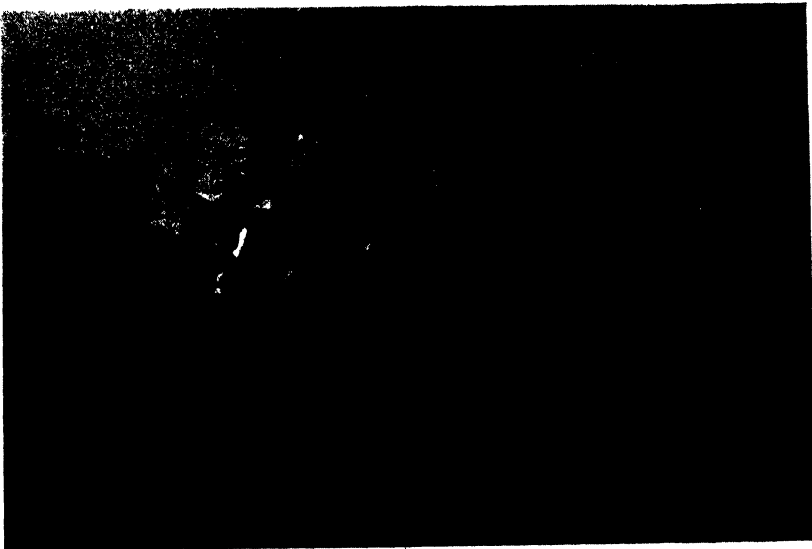


FIG. 1. *Lepomis auritus* wintering in a quiescent state in the New York Aquarium.
Photo by S. C. Dunton.

shut off for short intervals. Such action caused an immediate and complete dispersal of the school. This unexpected result is illustrated by figure 2, which was taken a few moments after figure 1, and shows the school in the early part of the process of dissolution. The immediateness of this effect precluded the possibility of any $O_2$ or $CO_2$ change being a causation.

Since it was already established that fishes freely suspended in water head into a flow of water for rheomorphic reasons, various modifications of the water inlet were made to further study the details of its effect. By

introducing the flow from the opposite side the school would, of course, turn to face it. Further than this it became apparent that the outlines of the school were all determined by the somewhat complicated flow lines in a



FIG. 2. The immediate dissolution of the wintering aggregation on an interruption of the current that determines its formation, shape and position. This photograph was taken a few minutes after Figure 1. Photo by S. C. Dunton.

rectangular vessel, including the various minor eddy currents. This was checked carefully by watching the course of suspended particles, and by suspending heavy cords to which were attached fine threads that wafted out more or less horizontally, depending on the strength of the flow, and pointed in its direction. In figure 1 the flow of water enters in the lower right-hand corner near the glass. It leaves at the surface (out of the photograph) at the rear of the tank near the upper left-hand part of the picture. The pyramidal form of the school seems to be accounted for by the fish seeking some rate of flow at which they can maintain their position, with a minimum swimming effort, at their low metabolic level at 5° C. The school has a flat base cut off by the strong horizontal flow across the tank bottom because of the low position of the water inlet. The induced flow that this stream causes in the body of the water is of less speed, but apparently the optimum is close to the surface of the main flow as measured in part by the thinning of the school toward the top of the pyramid. The question might be raised as to why the fishes do not seek a position of minimum flow. This is adequately answered by the fact that freely suspended fishes tend to be thrust forward by the backwardly directed flow of the exhalant water from their gill slits. While it is true that these sunfish can maintain a stationary position in still

water, they can only do it with an expenditure of energy in the use of their pectoral fins for " backing water " (Breder, '26).   It would thus appear that the form of the school is determined by the fish seeking a position of minimum effort.   The consequent crowding forces some into less desirable positions.   It also explains in full the immediate breaking up of the school on stopping the flow.   They move forward as against a current no longer present, and then maintain their haphazard position by an increased effort.

In experimenting with various positions of the inlet, it was found that practically any form of aggregation could be molded at will.   Thus, inverted pyramids were created by reversing inlet and outlet; oval groups by intermediate positions; a long horizontal axis by a strong flow, and a short horizontal axis by a weak flow, etc.

*Carbon Dioxide.*—In order to determine the effect of increased respiratory difficulties, $CO_2$ was introduced with the incoming water.   No dispersal of the aggregation was obtained on the concentrations tried, the school remaining as before.

After the flow was shut off and the school dispersed, as previously described, $CO_2$ was bubbled through the water.   This caused a definite re-aggregation of the school after a certain concentration was reached.[1]   When the school was broken up by mechanical means it re-formed rapidly so long as the $CO_2$ concentration was high.   The position and form of these aggregations were similar to, but not identical with, those caused by the flow of water.   The edges were more loosely defined and the centers of concentration only approximated those definite ones of the flow schools.   In the absence of other disturbing influences, it is thought that this resemblance may be due to habit formation.   Lest it be imagined that the stream of $CO_2$ bubbles induced a circulating current in the water, it is emphasized that these effects were apparent long after the $CO_2$ gas had been shut off.

*Mechanical Disturbance.*—Although the fish in the aggregation were quiescent and as near to a state of " hibernation " as such fishes ordinarily attain without actually freezing, they were still distinctly alert.   For example, it was easy to disrupt the school by casting a shadow on the fish by moving the hand over the tank.   This was repeated many times, causing the fish to scatter and seek the tank corners.   Re-formation of the school occurred in a few minutes.   Indeed, sudden movements or footfalls were necessarily guarded against in working about the aquarium when experiments were in progress.   Visitors peering through the glass from the exhibition gallery, however, had no effect on the aggregation.   This is not remarkable, for most of the fishes kept in these tanks become rapidly accustomed to the constantly present stimuli of passing throngs.

*Number of Individuals Necessary to Form an Aggregate.*—Experiments were performed to determine how many individuals are necessary to form

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[1] Concentration increased from 0.00 + mM. to 0.17 mM., pH dropped from 6.9 to 6.5, temp. 6.5° C.

an aggregation. Starting with two fish they were found to "aggregate" with each other after two days. This occurred between two *Lepomis auritus* in a tank of *Apomotis cyanellus,* the latter of which were never seen to aggregate. More *L. auritus* were added until there were eleven. Two aggregations were formed, one of four and one of seven. These finally merged. The presence of the *Apomotis* may have been somewhat confusing and may have delayed the schooling.

*Other Species.*—Other centrarchids kept under identical conditions, with the exception of *Micropterus* and *Acantharchus,* have not shown these effects of aggregation. One is congeneric—*Lepomis incisor* (Cuvier and Valenciennes). The others definitely noted are *Apomotis cyanellus* (Rafinesque), *Eupomotis gibbosus* (Linnaeus), *Chaenobryttus gulosus* (Cuvier and Valenciennes), *Ambloplites rupestris* (Rafinesque), and *Enneacanthus gloriosus* (Holbrook). *Pomoxis sparoides* (Lacépède) shows a very slight tendency to form large, loose aggregates.

Experiments were performed to determine the reasons for the observed differences in social attitude. Four *Lepomis incisor* were introduced to a tank of aggregated *L. auritus.* For three days they avoided the aggregation, resting in various positions about the tank as they previously did in the aquarium of their fellows. On the fourth day one of these specimens became part of the aggregation and, except for its recognizable physical differences, it might have been a *Lepomis auritus.*

Specimens of *Apomotis cyanellus* never merged with the aggregation, although they had opportunity to do so for fourteen days or more. As pointed out under the heading "Number of individuals necessary to form an aggregate," *Lepomis auritus* formed a school in the same aquarium.

## DISCUSSION

From the preceding experimental procedure and observations it is clear that temperature, light, and current must all be of a certain quantity for the formation of the over-winter aggregations of schools of *Lepomis auritus.* A too extreme variation of any one of these is enough to destroy the group.

If one attempts to classify this association according to ecological terminology, a confusion immediately confronts one. This is based partly on the inability to define effects and interpret their full significance, and is partly because of overlapping and vague borders of the terminology itself. A consideration of this terminology which involves a discussion of the classification of Deegener ('18) is reserved for another communication. Resigning for the present from an attempt to fit the phenomenon under consideration into such a classification, we may pass on to an interpretation of the results obtained experimentally.

*Temperature.*—In order to understand the apparent aggregating influence of low temperature on sunfishes, the normal behavior of such fishes in a state of nature throughout the year must be discussed. Beginning in the warmest

season, mid-summer, *Lepomis auritus* in common with other species of sunfishes may be found resting quietly, solitary for most part but not widely separated from one another, or in small groups. The breeding season has passed and the sex influence is at low ebb. The young fish have escaped from the influence of the male parent and may be found in small schools, *sympaedia,* or are in the process of forming the *sysympaedia* of Deegener ('18)—the *patropaedia* of the fishes having broken up. The formerly breeding fish are feeding and building up from the depleting effects of reproduction, while the year's young are growing rapidly and show the large appetites of most young fish. Such association as may be detected among the adults is probably purely of a tropistic nature, formed by the mutual seeking of satisfactory or optimum conditions. To some extent both adults and young may represent a *symphagium,* since their chief activity is that of feeding.

As the autumn sets in they seek deeper water, usually the deepest part of a small pond or lake, avoiding the ruffled surface waters of fall, and finally the ice. The food supply fails and their appetites decline with it as a result of the falling temperature. This movement may be thought of as a very ill-established, elemental sort of migration—a primitive *symporium.* In places as above described these fish remain until the warming influence of spring is felt, and meanwhile form groups identical with those studied in aquaria and described in the first part of this paper. Field observations from time to time on hibernating sunfishes give no hint of any differences between the wild fish and the groups studied in aquaria. These seem clearly to be the *syncheimadia* already discussed.

As warming takes place, the fish begin to move about, and when a temperature of about 16° C. is reached, the males seek the shallow shore line and start nest construction, as was shown by Breder and Redmond ('29) and others. These males, although seeking more or less communal, sandy patches in which to build their nests, represent a scattering movement compared with their over-wintering associations. The females remain longer in the wintering areas and then wander about until they are courted by the more energetic males. They thus pass from a *preconnubium* to a *connubium simplex.* Since more than one female may mate with a single male—and possibly one female may also deposit eggs in the nests of more than one male—there may .be *polygamy, polygyny,* and *monogamy* existing side by side, but it could scarcely be considered a *communal connubium* due, in part at least, to the limits of sexual ability by which these fishes are bound. After this phase has passed and the young have escaped from the *patropaedium,* the cycle as described is complete. Such is the general background against which this study of the wintering aggregation rests.

So far as the year's fish are concerned, they are apt to winter in a separate place from the adults, in part at least, for reasons set forth under "current," because of their smaller size. These aggregations may be considered *sysympaedia* and continue more or less until the water warms suffi-

ciently to permit greater activity. In very small ponds with dense population in which wintering quarters are at a premium, the various sizes may be all together in a *synchorium* composed of false *sympatrogynopaedia* wintering in a common *syncheimadium*. In the light of the above and preceding experiments, the influence of the temperature factor appears first as a quieting effect, because of physiological inhibition and the seeking of a common optimum hibernium. This, of course, is common to all sunfishes in northern latitudes, as well as the generality of fresh-water fishes under such environments. It explains nothing, however, of the nature of the aggregation displayed by any one species. Such details must be referred to other influences.

*Light.*—Since a certain amount of illumination is necessary for the fishes to see each other, it follows that the form of the school becomes vague at night and reconsolidates each day. This was demonstrated experimentally and indicates that vision is the primary, if not the sole, means of integration. It also indicates that the form of the aggregation is kept intact only by continual slight muscular adjustments on the part of the individuals composing it. This factor in no way explains the shape that the aggregation takes, but is simply the physiological basis making the aggregation possible. Thus the form assumed must be referred to other factors as to the fulfillment of some obscure " psychic urge," such as suggested by Parr ('29) for mackerel and by Spooner ('31) for *Morone*.

*Current.*—The effects of current are made evident in several ways. Primarily the force of current rules out certain places as resting sites and to that extent the aggregations may be considered as mechanically forced together in *synaporia,* and to some extent as *synchoria.* The relationship of perfectly still water to resting fishes, because of the forward resultant of the respiratory flow, has already been discussed. This condition further assists in the formation of the aggregations, but from the negative side. In order for fishes to maintain themselves in a flow it is essential that they line up with it and present a minimum resistance in accordance with their " streamlined " form, as already noted. This accounts for their all facing the same way, as shown in figure 1. For this condition, coupled with the preceding, there seems to be no term, but in accordance with the multiplicity of terms already manufactured it might be designated a *rheoporium.* The immediate breaking up of the aggregation on a cessation of the flow thus becomes clear. As already indicated, the fishes primarily continue their respirational " swimming " against the no longer existing current. By the time they have recovered their equilibrium and returned to a steady state in the now still water by greater muscular effort, the aggregation is dispersed. Viewed this way, as we have shown, the aggregation receives its determination of shape from the nature of the flow in which it takes form.

As previously explained, all centrarchids do not aggregate after the fashion of *Lepomis auritus*. Its congener, *L. incisor,* a closely related species, is an outstanding example. The explanation apparently resides in the fact

that this species seeks more nearly still waters for over-wintering. In an aquarium there are numerous but scattered eddies and places close to the tank walls in which the fishes fit themselves. Thus for some reason not perfectly clear, but probably referable to small differences in structure rather than a psychic one, apparently it is more effortless for *L. incisor* to maintain a stationary position in almost still water than in a slight flow. To avoid any possibility of the influence of aquarium differences during the experiment, the fishes of a tank of *L. auritus* and a tank of *L. incisor* were interchanged. As soon as they recovered from the shock of handling, each species arranged itself as before; that is, *L. auritus* aggregated and *L. incisor* did not.

From the above it would seem that the aggregation of *L. auritus* was purely mechanical and had no social implications whatever. Assuming that two or more fish find themselves holding a desirable position in a flow, more or less side by side, driven there primarily by the environmental influences already sketched, there is good reason that they should cohere. It is a well-known fact that fishes hold their position in a current by maintaining a constant pattern on the retina. If the view tends to drift ahead, relatively, they make appropriate compensating movements. Thus, in this case, the most evident " stationary " object would be the nearest fellow and they would mutually gauge their position by each other. The fact that there is a mutual interaction adds to the effect of the common impulse and of a superficially apparent social effect. Incidentally, a single *L. auritus* alone in an aquarium usually hugs the walls as closely as it would a fellow. *L. incisor* generally does this also, for other reasons previously explained. The breaking up at night of such a school would then simply be due to the inability to see an object by which to gauge their position, resulting in a consequently less perfect integration accompanied by a loss of position. This entails the corollary that more muscular effort is expended in the dark than in the light by these resting fishes.

Considered in this connection, the mackerel school, studied by Parr ('27), and the herring by Breder ('29), hold their relative positions in a similar fashion, as was indicated by those authors. The apparent difference is simply that in the present case the water is flowing past the fish, and in the mackerel and herring schools the fish are driving through the water and thus produce their own relative flow.

The adoption of one *L. incisor* out of a possible four by a school of *L. auritus*, as described in one experiment, also becomes clear. It is inferred that the one simply picked up the school as a point of integration, while the other three used the opaque walls for this purpose. It is to be again noted in this connection that the distance between fish and fish, and wall and fish, was found to be essentially the same in all cases.

*Carbon Dioxide.*—The effects of $CO_2$ as a cause of aggregation in *L. auritus* is somewhat puzzling, but when considered in connection with other studies becomes rational. It is to be noted that this experiment is purely

ificial, because under conditions of hibernation, with low temperature and
· respiration, suffocation never becomes a factor in a state of nature.
is is not so in the case of aestivating cichlids studied by Breder ('34).
ese fishes, given to much fighting, simply rest side by side when the $CO_2$
.centration reaches a certain level. There is no current in their stagnant
ldles or in balanced aquaria, and consequently no marked formation of a
ool heading one way, but their centrifugal reactions to one another are
ibited and they more or less huddle together. This also occurs in a state
nature and Breder attempted to ascribe to it a survival value. In the
sent case, which does not occur naturally, the effect is nevertheless similar,
sing an aggregation. The resemblance of the $CO_2$ aggregations to the
irrent " aggregations of sunfish, we would refer to associative memory,
the experiments were performed immediately after the break-up of the
rent aggregation.

General observation show that suffocating or nearly suffocating fishes,
·ering near. the surface of pools, ordinarily occur in groups more closely
·regated than normal, or at least are as close as they commonly approach
h other. It may thus be that adverse influences tend to cause aggrega-
is generally. This would seem to be in accordance with the work of Allee
1) and Allee and Bowen ('32) on the influences of toxic substances. In
eral, they have attempted to ascribe survival value to such behavior. In
present case, however, there would seem to be none, and we see no reason
believe there necessarily is any, except in a very indirect way as in the
cial case of Breder's cichlids, because of the marked fighting proclivities.
would seem that such aggregations may be useful, neutral, or harmful to
ier individuals or species, or both as has been indicated by Allee.

It has been indicated by Eddy ('25) that certain stimulants cause aggre-
ion and certain depressants cause dispersal in young *Ameiurus*. Shelford
l Allee ('14) showed that the reactions of fishes to gradients of dissolved
es were in part referable to rapidly " conditioned " responses on the part
the subjects. Both of these items suggest further study of the effect of
$_2$, involving the use of various concentrations and the separation of
ditioned responses.

*Fish Schools.*—The formation of any fish school has been looked upon
a special development of social behavior of a positive sort appearing in
ious places under different guises. Considered this way it is difficult to
thesize the entire set of phenomena under a uniform concept, since there
·ays remains a variety of special cases that need particular explanation.
however, one invert the concept and erect the hypothesis that all fishes
primarily impelled to seek other moving objects (other individuals of
ir own kind would naturally most often present themselves), and that in
cases where this effect does not display itself there is some inhibiting
uence at work, the question may be fairly answered. It is obvious that a
t of influences could act as inhibitors. A few cases and examples will

serve to explain the view.   The cichlid *Aequidens* discussed by Breder ('34) starts life in a closely integrated school and individually will respond positively to any moving object its receptors are capable of detecting.   This habit later becomes overlaid by a centrifugal influence under the stimulus of the developing gonads and does not appear again under normal conditions.   If, however, experimentally or under natural conditions, adverse factors appear (*e.g.* too high a $CO_2$ concentration), the centrifugal influences disappear and the fishes are at least neutral to each other, if not feebly attracted.

Again in the case of *Lepomis auritus,* life starts in a school similar to those of the cichlids and does not break up until feeding or gonadial activity disrupts it.   Each winter thereafter, with a reduction of the feeding and sexual impulses, aggregations or schools re-form, as discussed in the present contribution, only to break up when a rise in temperature allows the feeding and reproductive impulses to operate.   Mackerel, herring, etc., spend their entire lives in schools but here the feeding and reproductive habits do not run counter to it, both being communal activities.   Other forms, such as *Petromyzon,* spend their very early youth in aggregations, only to scatter out as soon as they take on their peculiar quasi-parasitic habits.   When the reproductive urge overtakes them, they again foregather, although here the effects of actual individual mating inhibit a true school formation.   According to Spooner ('31), *Morone labrax,* when young, shows its strongest schooling instinct, and this diminishes in intensity with the approach of the summer season, and also with feeding.   Mild, but not disrupting fright (adverse influence) aids in the re-formation of schools.   This mild fright reaction also occurs weakly in our sunfish during the summer months, or where aggregation is not present.

If we examine such fishes as *Lebistes* or *Fundulus,* that live in close aggregations, the effect is the same but the superficial physical appearance is different than—say the mackerel.   The latter are always forging ahead and are consequently oriented in a common direction—the typical fish school in the restricted sense—whereas individuals of the former may point in any direction.   Such a school does not primarily aim at going anywhere, the members being " browsers," not plankton feeders, with the consequence that individuals point primarily at scattered food objects.   Observe them, however, in a current, as *Fundulus* in a tideway, and they are found to present as well-integrated a school as mackerel.

It is inferred that schools of various fishes mix when they are sufficiently alike in habits to make it possible.   Unlike fish may also group together. For example, *Seriola* will follow sharks or other objects but stays with them only if the latter swim at a speed comfortable to it.   While the exact demonstration of the identity of all cases of heterogeneous assemblages must await further study and analysis, there is no reason at this writing to assume that it is conditioned by other than the simple working out of the basic principle: that is to say, the fishes primarily hold a position of maximum " comfort " by

fixing their vision on some object, either a stationary one or a moving one, this difference determining whether or not the fish maintains a stationary position or swims forward.

Overlaying this primary reaction, as illustrated above, are the immediate responses to various appetites which may intensify or be opposed to the primary reaction. In the latter case, owing to circumstances of internal necessity and environment, the holding of the position is neutralized. The chief influences inducing such effects are naturally the feeding and reproductive habits. If there are also other causes, they are not evident at this time. Parr ('31) has pointed out the relationships between the schooling habit and sex dimorphism in fishes. His main conclusion is that the schooling habit exists in inverse ratio to sexual dimorphism to as great an extent as other influences allow. Considered from the present view, the brilliant colors of males acting as mutual repellents, as in *Gasterosteus*, simply neutralize the fundamental attraction of fish to fish among that sex. In forms that have slight sex differences, as *Aequidens*, sex recognition is not so clear cut, as already explained by Breder ('34). It thus becomes apparent that if schooling is considered as a primary reaction, as based on the visual stimuli concerned with maintaining a position, the other effects, considered as inhibitors of this, become readily explainable. If, on the other hand, schooling is considered as a special social instinct, a synthetic explanation of the habit is practically impossible. Whether or not the habit is of importance to the species becomes secondary, so long as it does not become positively disastrous. When necessary it seems to have been inhibited as the need arose.

Without attempting to press the idea too far, the question may be raised concerning the utility of animal aggregations in general. Allee interprets the available evidence as indicating that aggregations frequently have a survival value. In some cases they are without doubt of value, but in others it is difficult to think of them as other than automatic responses that may be valuable, neutral, or fatal as Allee has recognized. One would naturally expect to have more of the former two surviving to-day, although, especially under laboratory conditions, numerous cases of the third could doubtless be devised. One need but think of the aggregating of fishes in response to a $CO_2$ increase.

In order to clarify the present concept of fish aggregation, including the fish school, a diagram (Fig. 3) has been devised. If the horizontal axis be considered as ontogeny, from hatching, through growth, maturity, reproduction, and the post-reproductive rest, while the vertical axis be considered the degree of strength of the impulse to form a school, a series of lines then may represent the effects as found in various fish species. The horizontal line at the top marked "1" represents fishes that remain in a school throughout life, completely schooling species, such as mackerel, herring, codfish, etc. The line marked "2" represents those that scatter out and become neutral to each while growing and feeding, only to aggregate for purposes of reproduc-

tion and that again disperse, such as *Petromyzon,* sturgeon, carp, pickerel, etc. Line " 3 " represents the fishes that start life in a school and scatter out, becoming positively repelled by others, and then aggregate again after the
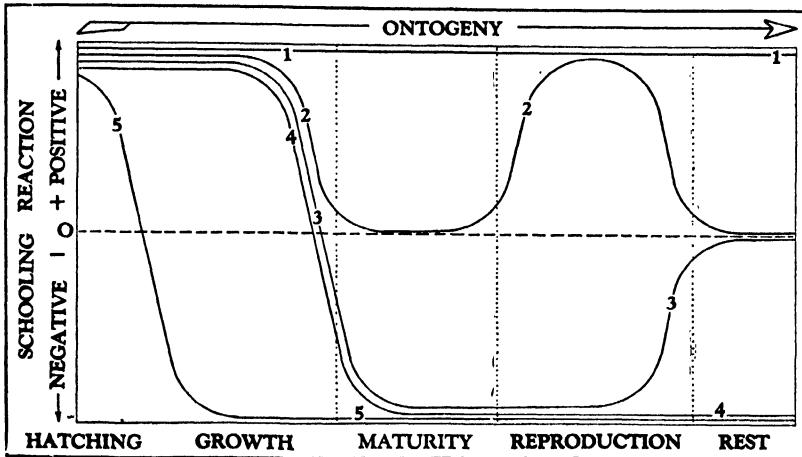


FIG. 3.  Schematic diagram of the suppression of the schooling effect in various patterns of fish habit.  See text for explanation.

reproductive season has passed, such as *Lepomis,* catfish, etc.  Line " 4 " represents fishes that start out as in the case of " 3 " but never again congregate in schools, such as *Aequidens, Betta,* etc.  The differences between this and " 3 " are probably due mostly to climate, " 3 " representing the effect of cold weather on what might have been the condition in " 4." Line " 5 " represents those that scatter out from hatching and never reassemble in masses, such as *Pterophryne* that are presumably cannibalistic from the smallest sizes.

Obviously this diagram shows only extreme cases and probably most species would fit between the lines drawn, as well as show numerous minor variations.  Only those that pass below the zero line into the " negative " range are fighters, that line simply representing neutrality.  This diagram cannot be extended too far and is intended for illustrative purposes only, proper diagrammatic treatment being impossible until such time as a considerable mass of really quantitative data are accumulated by some suitable technique not now available.  It is understood, of course, that these curves representing a depression of the schooling impulse may, in some cases at least, be raised by the occurrence of adverse conditions.

## SUMMARY

1. Winter aggregations of *Lepomis auritus* are purely mechanical assemblages conditioned by (1) temperature and the consequent lowered metabolic rate, inducing less activity; (2) light, vision being necessary to their con-

tinued existence, making possible the detection of points of observation for holding a position; (3) current, the seeking of a position of minimum physical effort.

2. The lack of aggregation on the part of *Lepomis incisor* is due to the seeking of the more disperse and more nearly stagnant areas by this species.

3. The apparent adoption of an occasional *L. incisor* by a group of *L. auritus* is due to the interaction of the effects mentioned under items 1 and 2.

4. Fishes maintain a stationary position in a flow by virtue of visual reference to some fixed object, and in a school by the same reactions, in which case, however, the point of reference moves forward. Schools may thus be primarily established by similar individuals finding the same optimum locations.

5. As based on the above, schooling may be considered as a primary impulse, with cases of non-schooling as inhibitions of it, caused by feeding, reproduction, or other requirements. Any cessation of such influences causes an immediate reappearance of the schooling habit.

6. Adverse conditions, generally, allow aggregating effects to appear. The results to the individuals and species may be valuable, neutral, or harmful. For example, temperature, light, $CO_2$, fright, and various toxic substances will cause aggregation.

7. The primary urge to aggregate, except as inhibited by definite influences, or secondarily released by adversity, may have general application.

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# CUTTING TREATMENTS OF ALFALFA IN RELATION TO INFESTATIONS OF LEAFHOPPERS

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Reduced populations of certain insects which feed upon agronomic plants are, at times, made possible by relatively simple cultural practices. Such has been the case (Graber, *et al.,* '31) with white grubs (*Phyllophaga* spp.) where egg-deposition of the adults and subsequent injury from resultant grubs may be profoundly diminished in definite areas by the culture of certain legumes and by a favorable environment for the subterranean growth of certain plants upon which the grubs feed.

More recently the writers have found that the time of cutting the first crop of alfalfa in Wisconsin has a most significant bearing on the numbers of leafhoppers which may prevail in the subsequent growth. This is given verification and explanation in this paper which describes the cutting treatments of alfalfa and the determinations of populations of leafhoppers in such alfalfa. Cutting treatments and leafhopper infestations are very definitely associated with the productivity of this forage.

That the leafhopper, *Empoasca fabae* Harris, is a direct cause of " alfalfa yellows " has been shown by Granovsky and Jones ('27) and its feeding habits, biological aspects and pathological symptomology have been described by them, and by Poos ('31), Jewett ('29), Monteith and Hollowell ('29), Osborn ('32), Fenton and Hartzell ('23), Smith and Poos ('31), and other workers. The feeding of this insect causes a yellowing of the leaves. Especially, when the insect occurs abundantly on alfalfa at early stages of growth is there not only a yellowing of the leaves but also a retardation of internodal elongation. These along with other factors including the early cutting of the first growth of alfalfa during 1932 and 1933, resulted in a reduction of seasonal productivity (as determined by the writers) ranging from 24 to as much as 57 per cent. In Wisconsin, where alfalfa is rarely cut more than twice annually, the losses directly ascribed to the leafhopper occur principally in the second growth. Usually they are not prominent in the first crop of hay or with the third growth.

Leafhoppers are not generally found in alfalfa fields near Madison, Wisconsin, until about the latter part of May or the forepart of June. Because at this time, the relatively small populations are primarily adults and because the internodal elongation and leaf development of the alfalfa has reached an

advanced stage (near blossoming) thus providing an abundant feeding area during the early period of the infestation, the injury from the insect is usually of minor consequence with the first cutting of hay. But if the first crop of alfalfa is allowed to mature seed or to arrive at the seed stages of growth, severe losses may result from the adults and their progeny.

## FIELD ASPECTS OF LEAFHOPPER INJURY

In the course of extensive field observations of alfalfa culture in Wisconsin from 1911 to 1921, the senior author (Graber, *et al.*, '33) observed in certain years a pronounced stunting and yellowing of the second growth. This seemed to be associated with early cutting of the first crop and also appeared to be augmented by previous winters which had injured the alfalfa. To verify the former he conducted an experiment in 1922 (following the injurious winter of 1921–22) in which the first growth of alfalfa was cut four days earlier than that of similar alfalfa only six feet away. With only such a minor difference in the time of cutting the first crop, the succeeding growth of the early cut alfalfa turned yellow and became stunted. This condition was in sharp contrast to the tall green alfalfa which followed the cutting of the first crop four days later. At this time such responses were not fully understood but as a result of the work of Granovsky and Jones ('27) who established the fact that leafhoppers are directly responsible for stunting and yellowing of alfalfa, the writers endeavored to determine more specifically the influence of the time of cutting of the first crop on leafhopper populations and injury in the succeeding growth.

## CUTTING TREATMENTS AND GROWTH RESPONSES

Two parallel strips of Canadian variegated alfalfa extending north and south and about a rod apart were seeded on June 27, 1930. The first strip (east) was 16 feet wide and the second was 22 feet wide. Each strip was divided into 12 plats, 35 feet in length. A third parallel strip (a rod west of the second strip) similar in length and 22 feet wide was seeded to plats of five varieties of alfalfa. It was not used in this experiment but because it, probably, had an effect on the leafhopper populations in the first two strips of alfalfa it will be given reference later. Alternating halves of each of the 24 plats comprising the first two strips of alfalfa were cut with a field mower on June 8, 1932, and June 9, 1933, when about one-tenth of the blossoms had appeared. The remaining halves of each plat were cut 12 days later on June 20, 1932, and June 21, 1933, when the alfalfa was near the full bloom stage. For convenience such areas will be designated subsequently as *A* and *B*, respectively.[2]

[2] It should be stated that while the 12 plats of the second strip of alfalfa had been fertilized heavily with phosphates and potash before seeding in 1930 and the first strip (east) had received no such treatment, good stands of alfalfa were secured in all plats.

The responses of the subsequent growth were similar in both years and for the purpose of brevity they will be described only for 1933. The second growth of the alfalfa cut early (*A*) had recovered and the stems were about 3 to 4 inches tall on June 21 when the remainder (*B*) of the first growth in the plats was cut. During the first week in July, the second growth of the alfalfa on areas *A* showed definite symptoms of yellowing and stunting. This became intensified until the third week of July when a sharp line of contrast prevailed between the second growth of alfalfa in areas *A* and *B*. At this time the alfalfa which had been cut on June 9 (*A*) and which had had 12 days longer for growth, was only 5 to 6 inches tall, sparsely blossomed, and very yellow. Immediately adjacent the alfalfa which had been cut on June 21 (*B*) was from 14 to 16 inches tall, abundantly blossomed, and of a healthy dark green color. However, during the last week in July the latter alfalfa began to show definite yellowing. The second growth of all plats was cut on July 31. Yields were determined. While they were profoundly affected by the degree of leafhopper injury, a presentation of such data will be deferred, as it is the purpose at this time to correlate leafhopper migrations and propagation with the symptoms and cutting treatments just described.

To ascertain the populations of leafhoppers (adults and nymphs) counts of the insects collected in five uniform sweeps with an insect net were taken on each of the alternating halves (*A* and *B*) of each plat during 1933 (table I). In order to condense these data an average of such determinations was taken for the 24 areas designated *A* and likewise for the 24 areas designated *B*. Except for the sweeps taken just after cutting the counts were made at times when most of the leafhoppers appeared to be well above the surface of the soil. Such determinations of the populations while not absolute were averages of counts made on 24 areas. They are, at least, comparative particularly when prominent differences occurred. Identifications were made on two samples of the insects by Dr. F. W. Poos and Dr. A. A. Granovsky [3] who found that they consisted almost entirely of *Empoasca fabae*.

Three seasonal cutting treatments were applied during 1931, 1932 and 1933 to quadruplicated and randomized plats in the fertilized and unfertilized strips consisting of (1) two summer cuttings (2) two summer cuttings and one late fall cutting (3) two summer cuttings and two fall cuttings. The only variations in these cutting schedules for the leafhopper studies were applied in 1932 and 1933 when each of the plats was sub-divided into two halves (*A* and *B*) and the first growth of one, series (*A*) was cut twelve days earlier than the remaining halves *B* as described above. Since the leafhopper populations were primarily associated with variations in the time of cutting the first growth the limited relationships of infestations to fertilization and to fall cutting treatments is not discussed at this time.

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TABLE I.  *Average of 24 counts of the total leafhoppers collected in an insect net with 5 uniform sweeps over each of 24 areas of alfalfa (A) the first growth of which was cut early and an average of 24 counts on 24 adjacent areas (B) where the first growth was given deferred cutting.  These determinations were made at various intervals during 1933.*

| Date 1933 | A First cutting on June 9 | | B First cutting on June 21 | |
|---|---|---|---|---|
| | Adults | Nymphs | Adults | Nymphs |
| May 20 | .4 | | .4 | |
| "   25 | 1 | | 1 | |
| June  1 | 2 | None | 2 | None |
| "    6 | 17 | | 29 | |
| "    9 | 29 | * | 29 | |
| "    9 | First cutting A | | | |
| "   10 | 0 | | 51 | * |
| "   12 | 0 | None | 63 | |
| "   17 | 6 | | 59 | |
| "   20 | 49 | | 69 | * |
| "   21 | | * | First cutting B | |
| "   22 | 161 | | 0 | |
| "   24 | 156 | | 0 | None |
| "   29 | 99 | † | 19 | * |
| July  4 | 17 | | 13 | |
| "    4 | First prominent appearance of nymphs in A | | | |
| "    9 | 32 | † | 44 | † |
| "   15 | 220 | 2586 | 90 | 88 |
| "   24 | 948 | 579 | 940 | 168 |
| "   28 | 422 | 232 | 441 | 170 |
| "   31 | Second cutting A | | Second cutting B | |
| Aug.  1 | 3 | 8 | 3 | 11 |
| "    3 | .2 | .5 | .2 | 1 |
| "   10 | 2 | 1 | 3 | .2 |
| "   16 | 3 | 2 | 3 | 0 |
| "   25 | 17 | 1 | 15 | 0 |
| Sept.  1 | 7 | 2 | 11 | 1 |
| "   18 | 7 | 21 | 10 | 25 |

\* A few nymphs were caught in the sweepings on these dates but counts were not made due to small size and injuries in collecting.

† Nymphs became much more numerous but were not counted until July 15.

## LEAFHOPPER POPULATIONS AND MIGRATION

Adult leafhoppers first appeared (table I) in the alfalfa on May 20.  The numbers (.4 to 2.2) were very small during the next ten days but on June 9 they had increased to 29 on each half (*A* and *B*) of the 24 plats.  No nymphs were observed.  No material injury to the alfalfa was evident.

On June 9 one-half (*A*) of each of the 24 plats was cut and the undried hay was removed immediately.  The day following no adults were found in the sweepings of the cut areas (*A*) but in the adjacent uncut alfalfa (*B*) the leafhoppers had increased from 29 to 51.  According to the counts made on June 10 (table I) a migration of the adults had occurred from the areas where an abundant food supply had been removed to the adjacent source of food,— the uncut halves (*B*) of the 24 plats.  Some yellowing of this alfalfa (*B*) occurred but the injury was not of material consequence.

After eight days the alfalfa cut on June 9 had recovered and had produced a second growth of from 2 to 3 inches in height. At this time (June 17) only 6 adults were found in this young alfalfa (*A*) as compared with 59 in the old alfalfa (*B*) on the uncut portions of each plat. On June 20 the adults in the young alfalfa (*A*) had increased to 49 and in the old alfalfa (*B*) to 69. From whence these accretions in the populations of adults came was not determined definitely. The very rapid increments in areas *A* indicate a preference of the leafhopper for young rather than old alfalfa.

The day after cutting (June 22) the old alfalfa (*B*) and removing it, no adults were found in the sweepings of these cut areas, but in the young alfalfa (*A*) the adults increased from 49 on June 20 to 161 on June 22. Counts made two days later (June 24) showed no leafhoppers in the cut areas (*B*) but 156 adults in the young (*A*) alfalfa. The prompt shifts of the adult populations from the cut to the uncut portions of the plats is, again, clearly evident but the total numbers of adults in *A* and *B* are much increased from June 17 to June 24. The numbers may have been augmented by migrations from the parallel strip of varieties of alfalfa which had, also, been cut on June 21 [4] and possibly, by migrations from other host plants in that vicinity. Eggs may have been laid in the basal portions of the first growth the forepart of June and not being removed in the first crop of hay may have hatched into nymphs which were not captured in the sweepings until they developed into adults. In any event a concentration of the adults occurred in the young (second growth) alfalfa of areas *A* from June 17 to June 24. That this appeared to have a significant bearing on the subsequent populations of nymphs in this alfalfa and the resultant injury sustained by this alfalfa is made apparent with later developments.

Adults did not begin to appear in the new growth of the alfalfa (*B*) cut on June 21 until June 29 and then only 19 were found in the sweepings. On July 4 an average of only 13 adults were caught in five uniform sweepings of each half (*B*) of 24 plats. In this same period (June 22 to July 4) the adults in the second growth of the alfalfa which had been cut on June 9 (*A*) showed a marked decline from 161 to only 17 adults. The causes of this sharp decrease in leafhopper populations were not ascertained, specifically. It seems probable that a gradual cessation of egg-laying and a general senescence of the older adults occurred. Rainfall did not affect the drop in numbers of adults from 156 on June 24 to 99 five days later, because only a trace of rain

[4] That the latter took place is indicated by the fact that prior to June 21 the adults apparently arrived by migration from the east and were much more numerous in the alfalfa plats of the strip farthest east (about 3 rods) from the parallel strip of alfalfa varieties. During the first seven days after cutting on June 21, however, the adults were much more numerous in the second growth of areas (*A*) of the alfalfa nearest (one rod) to this source of migration. This parallel strip of varieties of alfalfa, was the only alfalfa in relatively close proximity to the alfalfa on which the cutting treatments were applied except for two small areas which were assigned to Prof. E. M. Searls, University of Wisconsin, for entomological studies of the leafhopper.

occurred in the interval between these counts. However, after the counts were made on June 29, 1.44 inches of rain fell that day and on July 1 and 2, the total precipitation measured 2.21 inches. This may well have been a factor in the acceleration of the decline of the adults from 99 on June 29 to 17 on July 4 in areas $A$ where nearly all the adults were concentrated. Suffice to say, such a decline with its reduction in egg-laying could greatly limit the populations of nymphs in the second growth with a deferred cutting of the first growth.

## NYMPHS ABUNDANT IN SECOND GROWTH OF EARLY-CUT ALFALFA

The first prominent appearance of nymphs occurred on July 4. At this time they were so small and tender that counts were difficult and a determination of numbers was deferred until July 15. But on July 4, it was very apparent that the nymphs were much more numerous in the second growth ($A$) which followed early (June 9) cutting. On July 15, 220 adults and 2586 nymphs were collected in the five uniform sweepings of this alfalfa ($A$) as compared with 90 adults and 88 nymphs in the adjacent alfalfa ($B$) which had been cut on June 21. This amazing difference in the numbers of nymphs in the second growth of alfalfa was scarcely more pronounced than the contrast between the short, yellow and unproductive second growth of the alfalfa cut on June 9 ($A$) and the luxuriant second growth immediately adjacent where the first crop of alfalfa ($B$) was removed on June 21 or 12 days later. While the time of egg deposition was not determined entomologically, it is probable that with delayed cutting (June 21) of the first crop, the adults had laid most of their eggs in the tissues of the top growth before cutting. and that such eggs were largely removed in the first crop of hay. With only 88 nymphs (July 15) in the second growth of alfalfa in portions ($B$) of the plats compared with 2586 nymphs in the second growth immediately adjacent ($A$) it may well have been that egg-laying was not abundant in the new second growth of areas $B$ but occurred primarily in the new growth of the earlier cut alfalfa. To a considerable extent this may have been due to the migration of egg-laying adults from areas $B$ and from nearby plats given deferred cutting, to the young second growth of the alfalfa ($A$) which had been cut earlier. But aside from resultant migratory influences of deferred cutting on the density of nymphs in the second growth, the decline in numbers of adults (probably preceded by a gradual cessation of their egg-laying activities) during the latter part of June, appears to have a significant bearing on the populations of nymphs to be found in the second growth. Such causal relationships need further investigation.

## NYMPHS CAUSE SHARP-LINE CONTRASTS

The clear-cut and sharp-line differences between the alfalfa in areas $A$ and $B$ of each of the 24 plats was most impressive during the middle of July

FIG. 1. Sharp contrasts in the degree of leafhopper injury of the second growth of alfalfa followed deferred (June 21) and early (June 9) cutting of the alternating areas of the first growth.

(fig. 1). The young nymphs were found to be relatively static, appearing to migrate for only short distances. It is this characteristic along with the difference in numbers in the alternating areas (*A* and *B*) which accounts for the sharp-line contrasts observed in the plats of alfalfa, as well as in large fields which were investigated on several farms. However, such nymphs ultimately develop into adults and migration then takes place. This is shown by the population counts on July 24 when 948 adults and 579 nymphs were found in the alfalfa areas *A* and almost an equal number of adults (940) and 168 nymphs were found in the alfalfa (*B*) which had been cut on June 21. This alfalfa began to show definite yellowing on July 24 although its growth was fully 15 inches tall and the plants were abundantly blossomed.

Four days after July 24 a marked diminution in the leafhopper populations was again evident. On July 28 the numbers had decreased to 442 adults and 232 nymphs in the early cut portions (*A*) of the plats and to 441 adults and 170 nymphs in the portions designated *B*. This may well have had an important bearing on the general absence of serious leafhopper injury in the third growth. The causes for this decline are not clear. If climatic, it is of interest to note that no rain fell on July 24 to July 30, inclusive. But on July 20 a trace of rain occurred; on July 21, .23 of an inch; on July 22, .38 of an inch and on July 23, .02 of an inch. After cutting the second growth on July 31, the populations of leafhoppers on August 1 were very small (table I) and this situation continued throughout August and September.

## DISCUSSION

Leafhoppers have caused in certain years considerable losses in the productivity of alfalfa fields in Wisconsin. This was true particularly during the past (1933) season when due to weather conditions, much of the first crop was cut early. In feeding on alfalfa, leafhoppers cause a yellowing of the leaves and, if numerous, in young alfalfa they greatly retard internodal elongation with pronounced reductions in productivity. In Wisconsin where alfalfa is usually cut but twice annually, such losses occur primarily in the second growth. With early cutting of the first crop they were very severe in 1933. It was a "bad leafhopper year." Not only did the populations appear large but when cutting treatments were applied to small plats it involved only short migrations of the adults. Willard ('30) reports a border-effect of a rod or so, of very intense leafhopper injury of the third growth following the early cut portions of the second growth of large areas of alfalfa. This occurs adjacent to the line of juncture between the early and later cuttings of the preceding growth. It is probable that in our experiment the short migrational distances involved with the small areas of alfalfa greatly intensified the contrasts in leafhopper populations and the injury to the second growth of alfalfa.

Observations of large fields of alfalfa in Wisconsin during 1933 and for

several years previous, have shown that leafhopper injury may be serious, when an entire field has been cut early, in which case a resultant yellowing and stunting of all of the second growth may occur. They have shown in a more striking manner, however, that when a portion of a field has been cut early and the remainder several days later only the second growth of the early cut portion of the alfalfa is severely stunted by leafhoppers. With the latter, a sharp-line and spectacular contrast generally prevails, for a time, between the short yellow and tall green alfalfa of the second growth.

A full understanding of the part leafhoppers play in such field reactions of alfalfa will not be available until much more is known about the migratory tendencies and egg-laying habits of the insect with respect to its various host plants. Further knowledge is also needed with regard to the survival of the adults after a sudden and almost complete removal of the immediate food supply of the insect by cutting and curing an entire field of alfalfa for hay. That deferred cutting of the first growth of alfalfa may not be always an effective control for leafhopper injury of the second growth in all latitudes is indicated by Willard [5] of Ohio and by Poos and Westover ('34) the latter of whom state that "each year at Arlington Experiment Farm (Rosslyn, Virginia) from May 10 to 16 until July 1 or later, there appears to be a continuous and general migration of this species into alfalfa, after which special periods of migration take place as potatoes or other favored hosts become less attractive as food plants." Observations in Wisconsin, however, indicate that the migrations which may occur into the succeeding growth after deferred cutting of the first crop do not appear to be of serious consequence with regard to immediate and direct injury or with regard to later injury resulting from nymphs hatching out of the eggs which such adults may have laid. Moreover, the adult populations appear to decrease rapidly during the latter part of June indicating a cessation or decline of the egg-laying activities of the insect at the period when deferred cutting of the first growth would normally occur in Wisconsin. With early cutting of the first growth egg-laying of the surviving and migrating adults seems to be continued abundantly in the succeeding growth of alfalfa and may result in large populations of nymphs which are the chief source of injury in the young second growth of alfalfa.

The survival of the adults is probably enhanced when a portion of a field of alfalfa is cut early and the remainder several days later because there is always available in that field an abundant supply of food and a place for egg-deposition to which the insects may migrate. According to the counts (table I) such migrations appear to be relatively prompt after cutting and chiefly in the direction of the existing food supply. They would tend to concentrate the adult population of the entire field into the young second growth of the early cut portions.

The extent and degree of leafhopper injury in alfalfa fields in Wisconsin seems to vary widely from year to year. Whether this is due to environ-

[5] Information to the authors.

mental factors affecting the plants or to factors affecting the insect or to both is not determined. From the standpoint of the plant, however, there is good reason to believe that the condition of the alfalfa resulting from a complex of such interrelated factors as previous cutting treatments, winter injury, food storage, *etc.*, have an important bearing on the degree of injury which may occur from leafhoppers in alfalfa. Amplification of this thought with supporting data is reserved for a subsequent paper. The significant feature of the data presented in this paper is the outstanding relationship which is established between the time of cutting the first growth of alfalfa in Wisconsin and leafhopper populations in and injury to the second growth. The authors (Graber and Sprague, '33) have previously reported a summary of these findings and subsequently their validity was further established by the simultaneous work of Searls ('34) who studied the problem from an entomological viewpoint.

## Summary

Because the simple expedient of deferred cutting of the first growth of alfalfa has long been recommended in Wisconsin as a desirable practice for preventing the stunting and yellowing of the second growth of this forage, an experiment was conducted in 1932 and 1933 to ascertain the relations of the time of cutting the first crop to populations of leafhoppers in alfalfa.

Leafhoppers did not appear in the alfalfa used in this experiment until the latter part of May and then only in small numbers. While the populations increased during June they caused but slight injury to the first growth, a situation in common with observations in Wisconsin extending over a period of several years. Because the internodal elongation and leaf development of alfalfa had reached an advanced stage (near blossoming) providing an abundant feeding area for the limited numbers of leafhoppers present during the early period of infestation, the injury (stunting and yellowing) was of minor consequence in the first growth. Previous trials had shown that if such alfalfa were permitted to mature severe injury of the first growth may have occurred from the adults and their progeny.

As is generally true the third growth of alfalfa in this experiment also escaped serious injury. In part, the declines in populations which were evident in this experiment during the latter part of July (before the second growth was cut) and during August and September may account for this situation.

In Wisconsin, serious injury of alfalfa from leafhoppers occurs primarily in the second growth and particularly when the first growth is cut early. With the prevailing practice in Wisconsin of cutting but two crops of alfalfa hay annually, the control of leafhopper injury has not involved complicated cutting schedules but rather a simple deferment in the removal of the first growth.

A twenty-eight fold increase in the populations of leafhopper nymphs oc-

curred in the second growth where alternating halves of the first growth of alfalfa in each of 24 plats were cut 12 days earlier than the remaining halves of each plat. Such an extreme difference in the populations in adjacent areas of alfalfa resulted in a marked and clear-cut contrast in the degree of leafhopper injury during July represented by a short yellow growth of alfalfa following early cutting and an adjacent tall green growth of alfalfa which succeeded deferred cutting. Such sharp-line contrasts in the second growth were due to the relative immobility of the nymphs as well as to the pronounced differences in their numbers. After they became adults in the latter part of July they migrated to the healthy adjacent alfalfa which was rapidly yellowed by their presence although the contrast in height of the alfalfa in adjacent areas still prevailed.

Deferred cutting of the first growth of alfalfa in Wisconsin apparently provided for a more abundant and complete deposition of eggs in such growth so that the eggs or the nymphs hatching from them were destroyed in the curing of the hay. A marked decrease in the numbers of surviving and migrating adults during the latter part of June and forepart of July would point to a decrease in egg-laying during this period when deferred cutting normally occurs in Wisconsin.

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# THE CONDITIONING OF A CHLORAMINE TREATED WATER SUPPLY FOR BIOLOGICAL PURPOSES [1]

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During the past year (1933–1934), much difficulty has been experienced in securing a good water supply for aquaria and for experimental purposes in laboratories of the department of zoology at the University of Illinois. Due to the excessive chlorine and ammonia treatment of the University water supply, fish and some invertebrates have died in large numbers. It is well known that hardy adult fishes are sensitive to over five-tenths of a part per million of chlorine. Our results show that some delicate species are even sensitive to a residual chlorine or chloramine as low as 0.05 of a part per million.

Several experimental attempts to remove the chloramine were made, and it is the purpose of this paper to sketch briefly the results of these experiments.

## CHLORAMINE TREATMENT

A number of investigators have observed that the presence of ammonia and nitrogenous organic compounds increased the bactericidal action of chlorine. This has been attributed to the formation of chloramine ($NH_2Cl$) according to the reaction

$$Cl_2 + NH_3 \rightarrow NH_2Cl + HCl.$$
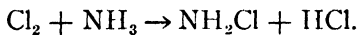
The chemical reactions between chlorine and ammonia have been studied by Noyes ('23) and co-workers and by Bray and Dowell ('20) who showed that in dilute solution chloramine was formed according to the reaction given above. Raschig ('10) has also shown that chloramine may be formed by the action of hypochlorite on ammonia. The chlorine in chloramine is in a similar state to that in hypochlorous acid, that is, it is an oxidizing and chlorinating agent. Its greater effect upon bacteria has been accounted for on the supposition that it is more soluble than chlorine and penetrates the bacterial cell more easily. It does not decompose spontaneously and therefore its entire strength is available for disinfection.

At the present time ammonia-chlorine or chloramine occupies a most prominent place in water treatment. This agent effectively destroys microorganisms, or effectively oxidizes objectionable organic compounds due to the presence of plants or industrial sewage in the supply. The treatment

[1] Contribution from the Zoological Laboratory of the University of Illinois, No. 457.

consists in adding ammonia or an ammonium compound and chlorine to the water, the two combining to form the chloramine.

Aquatic animals are kept alive with much difficulty in water treated in this manner, even though the dissolved oxygen be eight parts per million, *i.e.*, when the water is saturated with air at 20° C. In fact, such water is toxic to trout fry when the chloramine content is even as low as 0.05 p.p.m., killing the trout within 48 hours.

## REMEDIAL TREATMENTS

Remedial treatments were sought by (1) the dechloramination of the water with the use of chemicals; (2) prolonged boiling of the water; (3) aeration of the water by (*a*) atomizer spray, and (*b*) by porous artificial stone blocks (Filtros Plate) using compressed air; and (4) the adsorption of the chloramine upon activated carbon.

1. Thiosulfate is one of the oldest and best known means of removing minute amounts of excess chlorine and is very successful in removing the chloramine.

$$2Na_2S_2O_3 + NH_2Cl + 2H_2O \rightarrow Na_2S_4O_6 + NH_4OH + NaOH + NaCl.$$
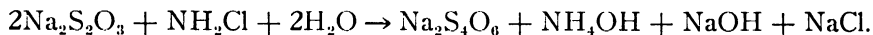
However, a standardized solution of thiosulfate is one of the reagents used for the determination of dissolved oxygen in water, and is likely to interfere with ordinary Winkler determinations if present in excess; and in many instances of experimental work as many as a dozen micro-Winklers are run in an hour's time. Lack of time, therefore, does not permit the operator to carry out the Rideal-Stewart modification of the Winkler method.

Sodium acid sulphite is a cheap and stable reducing agent, but it is an acid salt and its use is limited to waters which contain sufficient alkalinity to neutralize its acidity. This was successful with the water under consideration.

It was found that hydrogen sulphide could be added to the water in chemical-equivalent amounts and reduce the chloramine. A saturated solution of the hydrogen sulphide in water was added in small amounts to the tap water, and since the concentration of the hydrogen sulphide added was so very minute, the water did not prove toxic for the fish. If any slight excess of the gas remained in the water, it could be destroyed by aeration which is usually given the water before its introduction into the aquaria.

Other reducing agents such as ferrous salts and ethylene were tried and could be used. However, all chemical methods demand a rigorous chemical control, constant attention, and undue expense. Engineers and manufacturers would not recommend any existing feeding apparatus for use in supplies to laboratories.

2. To remove chlorine from water by boiling, Adams and Buswell ('33) found that it was necessary to boil for thirty minutes. Chloramine could not be removed when the water was boiled for three and four hours. We did

find that chloramine could be removed by first acidifying and boiling thirty minutes. This treatment, though, necessitates a re-adjustment of the pH and the expense of cooling the water before its use in the aquaria. A partial chloramine removal can be affected if the water is boiled three hours. Due to the high carbonate content in the University water, the effluent from the boilers had an average pH of 8.7. Here, we used (very effectively) the sodium bisulphite treatment, for the pH was high enough so that the final effluent after the removal of the toxic material remained at pH of 7.5.

3. Aeration removes some of the chloramine and for ordinary purposes might be an adequate treatment. In our case, however, where the chloramine content of the tap water was from 0.8 to 0.9 parts per million, after atomizer spraying there still remained 0.3 p.p.m. Forced aeration was accomplished by means of forcing compressed air through a block whose sides were of porous artificial stone, but this method was little more effective than natural aeration (table I).

TABLE I. *Showing the concentration and toxicity of Chloramine in the water supply at the University of Illinois between Jan. 1 and April 7, based on killing power. The Chloramine was determined by the ortho-tolidine method, and is reported as parts per million*

| Kind of Water | Average Chloramine | Fatal to | Maximum Chloramine | Fatal to |
|---|---|---|---|---|
| Tap | 0.76 | Hardy Minnows | 1.2 | Large carp, Bullheads, crayfish and invertebrates |
| Porous block aeration; two tank; long period | 0.3 | Trout fry instantly | 0.4 | Sunfish and some Bullheads |
| Porous block aeration; short tank period | 0.4 | " | 0.6 | Sensitive adults and trout fry instantly |
| Atomized by spray | 0.3 | " | 0.4 | " |
| Activated carbon and re-aeration | 0.01 | Lived two weeks [3] | 0.06 [2] | Trout fry in 48 hours |

[2] Rapid flow, overworking filter.

[3] Test discontinued after two weeks. Trout still very active.

4. The fourth method tried was the adsorption of the chloramine upon activated carbon by passing the water through a layer of such carbon in a gravity filter.

## ACTIVATED CARBON

In an effort to form some scheme which would afford a safe " wall " between the toxic water supply and the aquaria, which contained important animals, sometimes material of genetic experiments; the aquaria were furnished water with the installation of an activated carbon filter which very

successfully dechloraminates water. Chemical treatments of the water have disadvantages in that they require rigorous control and constant vigilance. Furthermore, the minute the injector fails, the water treatment is stopped and there is no longer a " buffer " between the water supply and the aquaria. The activated carbon treatment is simple, economical, and universally effective in the various waters one may have. It is a most excellent dechloraminator for a physical type of reaction.

Activated carbon is produced by high temperature distillation and subsequent chemical treatment of certain lignites. Lignite is a variety of coal intermediate between peat and bituminous coal. The particular and valuable characteristic of activated carbon is its high adsorptive capacity.

Adsorption should not be confused with absorption. While the former is a phenomenon that is not completely understood, it is believed that a loose chemical combination exists between the molecules of the adsorbent and the adsorbed substance. It is this property of adsorption that enables the carbon to attract to itself the minute particles of chloramine and retain them. Actually, it is not this simple, as the chloramine affects an oxidation after its initial adsorption. A well known illustration of the effectiveness of adsorption is the use of activated carbon in gas masks. Just as poisonous gas may be removed from air, so may chlorine compounds be removed from water by contact with activated carbon.

## Oxygen also Removed

Not only are salts and organic materials adsorbed onto the activated carbon, but dissolved oxygen is also removed, so when this treatment is employed the water must be re-oxygenated before its introduction into the aquaria tanks. This can be readily and cheaply accomplished by allowing the filtrate to trickle down slowly on a trough with a corrugated bottom as designed by Shelford ('29, p. 501). By this method we were able to put about eight parts per million of oxygen into the water at 20° C. (table II).

## The Filter

The experimental filter was made in a five-gallon glass aspirator jar. It produced an effluent free from chloramine at the rate of nearly a quart per minute. The jar was filled with a two inch layer of sand which was held up by a layer of fine gravel. Activated carbon was then placed upon the sand in a 6–7 inch layer and the bottle connected to the intake valve at the top. The effluent from the bottom of the jar was led from the filter to the aeration trough and then introduced into the aquaria. The rate of flow was controlled by the intake valve.

For very small aquaria for use in biological lecture demonstrations, experimental work, etc., one can easily prepare a small filter with a capacity of 75–100 c.c. per minute. A piece of cylindrical glass tubing 50 mm. in diam-

eter is fitted at either end with a one hole stopper and tubing and supported on a ring stand by means of a clamp.   This is filled with 5–6 inches of activated carbon.

TABLE II.   *Flow sheet for experimental carbon filter*

| Date | Hour | Temp. of water ° C. | Chloramine—PPM | | | Dissolved Oxygen —PPM | | pH | Rate of flow c.c. min. | Change in rate of flow |
|------|------|------|------|------|------|------|------|------|------|------|
| | | | Filter intake [4] | Raw effluent | Aerated effluent | Raw effluent | Aerated effluent | | | |
| 3-20-34 | 3 P.M. | 16.0° | .86 | .010 | .010 | .2 | 8.9 | 7.60 | 900 | |
| 3-26-34 | 3 P.M. | 20.0° | .76 | .010 | .010 | .3 | 7.6 | 7.53 | 900 | 0 |
| 3-30-34 | 3 P.M. | 18.0° | .86 | .015 [5] | .010 | | 8.5 | | 910 | 10 |
| 3-30-34 | 4 P.M. | 18.0° | .86 | .01 | .008 | .35 | 8.6 | 7.61 | 900 | − 10 |
| 3-31-34 | 3 P.M. | 14.8° | .96 [6] | .01 | .01 | | 9.0 | 7.60 | 900 | 0 |
| 4- 2-34 | 3 P.M. | 19.5° | .66 | .00 | .00 | | 7.6 | 7.65 | 800 | − 100 |
| 4- 3-34 | 10 A.M. | 18.0° | .76 | .06 | .06 | .3 | 8.5 | | 1900 | 1100 [7] |
| 4- 3-34 | 2 P.M. | 18.0° | .66 | .08 | .075 | | | | 1500 | −400 |
| 4- 3 -34 | 5 P.M. | 18.0° | .66 | .01 [8] | .01 | .3 | 8.4 | | 910 [9] | − 690 |
| 4- 7-34 | 1 P.M. | | .76 | .02 | .01 | | | | | |
| 4-13-34 | 3 P.M. | 14.6° | .76 | .00 [10] | .00 | .38 | 26.2 [11] | 7.58 | 200 | − 710 |

[4] Correction was made for color due to iron.
[5] Filter back-washed in A.M. for 2 hrs.   Trout fry control taken; see Table 1.
[6] Duplicated analysis.
[7] Trout fry control taken in this experiment.
[8] Filter back-washed for 30 minutes.
[9] Back to normal flow.
[10] Filter back-washed 15 min.
[11] Effluent was aerated with pure oxygen in a closed system.   Trout fry extremely active and energetic.

To back-wash either of these filters it is necessary merely to change the direction of flow.   Back washing is carried out, primarily, to loosen the filter bed which becomes packed after continued usage.   If the filter is shaken occasionally during the process of back washing (to aid in loosening the carbon particles), 15–20 minutes is ordinarily a long enough period for the operation. If a constant flow of water is required, two filters may be employed—one being used while the other is being backwashed.

## Self-Reactivated

When activated carbon is used for the removal of chlorine compounds, the adsorbed chloramine serves as an oxidizing agent and attacks the structure of the carbon and reactivates the surface with the liberation of carbon dioxide.

$$NH_2Cl + H_2O \rightarrow NH_4Cl + [O]; \text{ then } C + 2[O] \rightarrow CO_2.$$
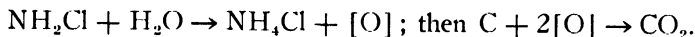
It is apparent that a slight wasting away of the carbon occurs, depending upon the amount of usage the filter receives; but additional carbon may be put in from time to time.

## Acknowledgment

The authors wish to acknowledge helpful suggestions given them by Professors A. M. Buswell and W. A. Noyes of the department of Chemistry, and Dr. D. Tarvin of the Illinois Water Survey. Thanks are also due Dr. D. H. Thompson of the Illinois Natural History Survey for supplying fishes and H. L. White of the University of Illinois Filter Plant for the installation of experimental spray heads and a supply of oxygen. The International Filter Company supplied the activated carbon.

## Summary

Chloramine has certain advantages over chlorine in water purification, but it is much harder to remove. When free chlorine is passed into water, it is a case of gas diffusion, but when chloramine is formed within the water, this latter is a case of a chemical compound dissolved in aqueous solution. Free chlorine may be removed by aeration or boiling with rapidity; but not so with chloramine. Aeration or boiling of such a water, for biological purposes, therefore, cannot be used.

Chemical removal methods include such reagents as: (a) sodium thiosulfate; (b) sodium acid sulfite; (c) hydrogen sulfide; (d) ethylene; (e) ferrous salts. Each of these has certain advantages.

A physical method involving adsorption and Freundlich's isotherm, is the removal of the chloramine with activated carbon. Table II shows the efficiency of such a method, where the effluent from the activated carbon filters contained 0.01 p.p.m. of chloramine when the initial water contained approximately 0.8 p.p.m. of chloramine. Oxygen is also removed from the water by this method, but can be easily restored again before its use in aquaria, etc.

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# AN EXAMPLE OF MYRIAPODS AS MULL FORMERS

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The main type of forest humus layer known as mull (Müller) seems, as a rule, conditioned by a fauna efficient in keeping down the fungi and maintaining a more bacterial type of decomposition (Müller, 1887; Falck, '23; and Romell, '34). In addition, this fauna may effect an extensive mixing of humus with mineral soil. This is most pronounced in extreme forms of mull such as the crumb mull (Romell and Heiberg, '31), inhabited by large earthworms.

At least outside Ramann's country, the rôle of earthworms in creating and maintaining a crumb mull type of humus layer has been rather generally accepted after Müller's classical studies (1887). Recently, this has been realized by Ramann's own pupil and successor, Lang ('31). On the other hand, the agents responsible for the formation of less extreme mull forms have remained obscure. Observations reported in the present paper suggest a rôle in the formation of certain mull forms to large myriapods of the American diplopod genus *Fontaria* Gray. The findings are believed to have some interest also for animal ecology. Prof. J. W. Bailey, of the University of Richmond, Va., has kindly informed me that most, if not all, work done on myriapods has been systematic in nature, with just a mention, here and there, of feeding habits, etc.

In localities with detritus mull (Romell and Heiberg, '31), large diplopods have repeatedly attracted the attention of Professor Heiberg and the writer and particularly of Mr. C. Heimburger, during his extensive field studies in the Adirondacks (Heimburger, '33). Specimens collected by Heimburger were kindly determined by Charles H. Blake, of the Boston Museum of Natural History, and by Charles E. Johnson, of the Roosevelt Wild Life Station at the N. Y. State College of Forestry, Syracuse, N. Y. They were found to belong to two species, *Fontaria trimaculata* (Wood) and *Fontaria coriacea* Koch (see Bollman, p. 123). Both species were described from northeastern United States by Wood, the latter one under the species name *corrugatus.*

In one particular locality, near North Hudson in the eastern Adirondacks, the largest species, *F. trimaculata,* was found to be very plentiful and exerting a most striking soil effect. The site is a steep south slope carrying a stand of middle-aged white pine with hardwood undergrowth and a ground vegetation of Heimburger's *Dicentra* type on a sandy loam rich in lime and showing a brown soil profile. More detailed data are given by Heimburger ('33) under

67

reference number 623. The humus layer showed an F horizon of varying thickness (for instance, a 2 cm F-layer under 3 cm litter), with white pine needles and leaves matted by white mycelia, and an H horizon of pronounced mull character but difficult to classify further. As a whole, the mull comes next to detritus mull in structure, but the organic matter content is low for this type of humus layer and the finely granular material is mixed with clumps attaining several cm in size. In spots with *Fontaria* particularly abundant, the large clumps formed a very considerable part or even most of the 6 cm H-layer. They were loosely layered and formed what could well be termed a super-crumb mull.                                                    .

The locality was visited by the writer together with Mr. Heimburger in October, 1932. Many of the Fontarias were at that time resting, tightly rolled up in their characteristic fashion. If the writer recalls rightly, some were found in the cavities to be mentioned later. The most interesting feature observed was the structure of the mull or earth clumps. Where the structure was well retained, the clumps invariably showed a great number of characteristic imprints, as seen on figures 1 and 2, but usually only on one side.
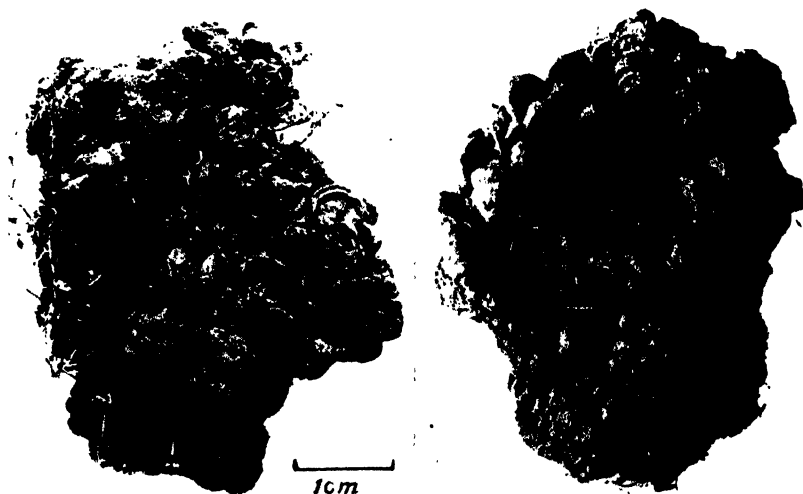


FIG. 1. Two of the largest excrement clumps of *Fontaria trimaculata* from North Hudson, N. Y.

On the opposite, "back" side, the clumps either mingled with the fine grained mull or loose earth, or they showed a warty surface. The clumps occurred in all sizes between a few millimeters and several centimeters and showed no particular shape, except that the larger clumps were mostly distinctly flattened, like a cake.                        .

The immediate inference from the findings is that the clumps are composed of excrements given off in a semi-fluid state and sticking together.

This interpretation was corroborated by observations in the laboratory on living *F. trimaculata* from North Hudson, kept in pots. They invariably gave off their excrements in the form of semi-fluid drops and left them with the characteristic imprint of their anus. The drops were either deposited singly,
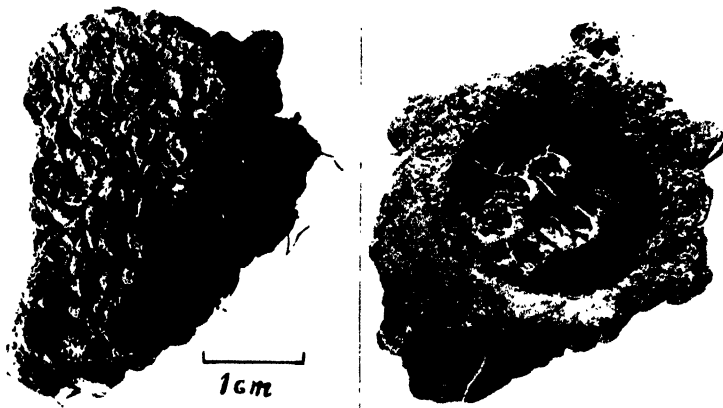


FIG. 2. Excrement clumps of *Fontaria trimaculata*. To the right a hollow clump cut open, with a more recent excrement clump in the cavity.

on earth, leaves or the walls of the pots, or they formed composite clumps; none were as large as the largest ones found at North Hudson, but otherwise they were quite similar.

The size of the imprints was always found the same all over any particular clump, but the size varied from clump to clump, as seen by comparing figure 1 and figure 2 which are on the same scale. Thus it seemed probable that even the largest clumps had been produced each by one single animal. This granted, the size of the clumps found at North Hudson is impressive, even though the animals may move around exceedingly slowly, so the clumps may be long in the making.

On microscopical examination at 1000 times magnification, the clumps as well as the surrounding fine grained mull were found to contain dead fragments of fungal hyphae and much other organic detritus, mixed with mineral granules. Living bacterial cells (*i.e.,* cells stained in the preparations) were more abundant in the fine grained mull than in the clumps. The organic matter content (loss on ignition) was found the same for both, averaging 27 per cent with variations from 25 to 28 or 29. This suggests a genetic connection between the clumps and the surrounding fine earth.

The pot experiments, already mentioned, were arranged so as to give some information on the feeding habits of the animals. Three earthenware pots were used, each about half filled with sifted soil from the upper mineral horizons of a podsolic forest soil (from hardwood forest of Heimburger's

*Viburnum* type in western Adirondacks). On the smoothed surface of the packed soil was placed in one pot a layer of fallen leaves of beech and sugar maple and in two pots first a cake of F-layer from North Hudson and then the fallen leaves of beech and maple on top. Two pots, one with and one without F-layer, received 2–3 living, about full grown *F. trimaculata*. The third pot served as a check. The animals did not thrive very well in any pot, possibly due to inadequate moisture conditions, and none lived longer than three months. A striking difference between the pots was apparent, however, during the first weeks, and it maintained itself to the end. In the pot with F-layer, the animals grazed on the white hymenomycet (clamp connections!) mycelium growing luxuriantly at the time on the cake of F-layer. Later, they fed also on the leaf litter which had in the meantime become softer although not attacked by the mycelium. They also disturbed the soil surface and produced a considerable quantity of excrements. The latter were the usual mixture of mineral soil and organic matter, dark grey in color, distinctly different from the brown soil which they covered, in the end, in an almost continuous layer. In the pot without F-layer, the soil was scarcely disturbed at all and little excrement was produced. The animals apparently starved to death rather than to feed on the fresh fall litter.

The observations seem to indicate that *Fontaria trimaculata* may be of considerable importance as a mull former, under favorable conditions. It is active both in interrupting an initial fungal type of decomposition (cf. Falck) and in producing an intimate mixture of humus and mineral soil. The same thing is likely to hold true for *F. coriacea*. Some other diplopods have been observed earlier to play occasionally a considerable rôle in the transformation of leaf litter into humus (Hoffmann, p. 415). It also seems that the myriapods, at least the vegetarian diplopods, quite regularly devour mineral soil, in addition to their supposedly main food (Plateau, 1876, p. 83), thus being of importance also as mixers, like the earthworms.

It remains an open question whether or not the Fontarias are important generally in the formation of the detritus mull with which they have been found associated. Thus far, the clear case reported from North Hudson stands isolated, and here the mull was not a typical detritus mull. The very characteristic excrement clumps have not yet been observed in other localities. This may be due simply to the unusual abundance of *Fontaria* in the North Hudson locality, but also to other reasons. Humbert (1872) observed that one and the same *Glomeris* can produce excrements of very different consistency and mineral soil content. Possibly the high lime content of the soil at North Hudson makes the clumps more resistant to weathering.

It should be mentioned in passing that the clumps observed at North Hudson clearly have nothing to do with the remarkable pill-making and nest-building activities noticed with different diplopods during the breeding season (Humbert, 1872 and 1893; Bailey). Most clumps are plainly mere excrement accumulations. Occasionally, however, large clumps were found hollow, containing a smooth cavity, open to one side, in size and shape fitting a

rolled-up *F. trimaculata*. One of these is shown cut open in figure 2. This cavity exceptionally contained a more recent excrement clump of a nearly full-grown specimen, as seen in the figure. The clump stuck loosely to the smooth wall and was apparently deposited by an animal which had stuck out its front end and begun to feed ere the hind end had left the cavity. Externally, the hollow clumps seemed to differ from the solid ones in nothing except in the presence of an opening. It seems likely that the cavities are resting quarters dug out in old excrement clumps just as they would be dug out in any suitable mass of soil.

The findings here reported have a bearing on a question of principle in the classification of forest humus layers. They clearly demonstrate the inadequacy of the definition of mull advanced by Bornebusch and, unfortunately, adopted by the International Union of Forest Research Organizations at the Congress in Nancy in 1932. Irrespective of how far the present findings go in explaining the origin of the detritus mull type, as it occurs widely distributed in the region studied, the observations at North Hudson show beyond doubt that there exists in nature mull forms, about as pronounced as they can be, which cannot be characterized as " consisting of or formed of worm casts." The earthworms have no monopoly on mull formation.

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# THE RELATION OF TEMPERATURE AND PRECIPITATION TO THE GROWTH OF BEECH IN NORTHERN INDIANA [1]

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Forest trees express in their growth as well as in their distribution an integration of a large number of environmental factors, among which temperature and precipitation are regarded by foresters and ecologists as of primary importance in influencing radial growth. In certain regions and with certain tree species these two factors exert a more measurable influence than in others. For example, in Florida the temperature factor does not appear to have an important effect on the diameter growth of longleaf pine, *P. palustris* (Lodewick, '30), while in Missouri (Robbins, '21) the sums of the mean temperatures for certain months have been found to vary inversely with the ring width of oaks. In both locations, however, a correlation exists between precipitation and annual ring width.

During the recent drought in the Central States which was aggravated by extremely high summer temperatures, the writer had an opportunity to collect additional data on the effects of these extremes on the radial growth of beech, *Fagus grandifolia* Ehrh.

According to Robbins ('21), Bogue ('05) determined the average width of the annual rings of 42 trees near Lansing, Michigan, for the years 1892 and 1904 and found a correlation between precipitation and width of annual rings. He states that an abnormally large or small annual precipitation is evidenced by the tree growth the following year. Stewart ('13) compared the width of the annual rings of an oak stump at York, New York, with weather records at Rochester, 25 miles north. Greater correspondence was found between variations in rainfall for June and July and ring width than between rainfall for the entire growing season and ring width. Brown ('15) working with *Pinus strobus* at Ithaca, New York, states: "The rapidity of growth is dependent upon three factors, moisture, available food (reserve), and temperature. The first two are at an optimum in the spring; the amount of growth therefore is directly proportional to the prevailing temperature."

Pearson ('18) compared the annual height growth of *Pinus ponderosa* saplings and the precipitation for various periods. He found that spring precipitation (April and May) was apparently the controlling factor. Factors reflecting the atmospheric conditions including evaporation showed a close though not consistent relation to height growth. The height growth varied inversely with the temperature probably because of the influence of temperature on transpiration and therefore on the relative water supply. Robbins ('21) measured the growth rings of the stumps of 16 oaks at Columbia, Missouri. A comparison of mean monthly temperature with the annual growth seemed to show that the annual ring width varies inversely with the temperatures for May and June. He found relatively high correlation between the total rainfall for the months of March, April, May, and June and the annual ring width. He also concludes that the dry spring of a given year shows its effect in that year's growth and not in the following year. Marshall ('27) studied the influence of precipitation cycles on the growth of western white pine, *P. monticola*, in Idaho. He found that the climate of northern Idaho as reflected by the growth of white pine indicates distinctly wet and dry periods, varying in length from 20 to 40 or more years. Douglass ('28) has done some interesting work on precipitation cycles and suggests the possibility of a correlation between sun spots and ring development. Burns ('29) in his study of the relation of rainfall and width of annual rings in Vermont forests states that there can be no direct correlation between rainfall and diameter growth because the width of ring at any one point is not an index to total increment and soil moisture is not a measure of rainfall nor of food supply. Lodewick ('30) in an investigation of the relation between certain climatic factors and diameter growth in longleaf pine in western Florida found no effect of temperature on wood production but a marked reduction or increase in precipitation was accompanied in most cases, by corresponding variations in ring width.

In the present study the beech was the species selected for two reasons, namely, because it has a rather shallow root system and consequently can be expected to reflect a scarcity of precipitation more readily than deep rooted species, and also because the beech-maple forest type approaches its western distribution in Indiana where one would expect such factors as moisture, temperature, soil, etc., to exert their greatest influence. During the late summer and fall of 1933 increment borings were taken from beech trees in seven beech-maple woodlands in the northern half of Indiana.

## METHODS

The technique used in carrying on this study was developed while the writer was working on a special problem in plant anatomy in the Department of Botany, Ohio State University. Samples were obtained from standing trees by means of an increment borer. In order to have adequate sampling and to eliminate the error of eccentric growth and the effects of shading and

FIG. 1. Increment cores prepared for measurement. The cores are glued into grooves of rabbetted lath and buffed down to bring out the annual rings.

crowding of other trees, three cores were taken from each of ten dominant trees in each of seven woodlands studied. The cores were taken systematically from the north, the southeast and southwest exposures and at four and one-half feet above the ground level. These cores were glued into the grooves of rabbeted lath (fig. 1), and were buffed down by means of a revolving electrically driven sandpaper disc. This treatment made the rings stand out so that they could be measured under the low power of a microscope by means of an eye-piece micrometer.

## PRECIPITATION AND GROWTH RINGS OF BEECH

From the measurements of the growth rings of beech in the present study, the average annual ring width of the 70 trees sampled (fig. 2) indicate that the average June temperature and total June precipitation have a marked effect on the diameter growth of trees. It is possible to pick out certain years which show definite minima and maxima which are common to all the woodlands studied. From figure 2 it is evident that 1915, 1924, and 1928 were excellent growth years, while 1914, 1923, 1925, 1931 and 1933 showed a marked decrease in the width of the rings. It is interesting to refer to the weather summary for these years in which high and low diameter growth took place. When one plots rainfall data by months and groups of months, a direct correlation between growth and precipitation for the month of June is found for certain woodlands, but not for others. The reason for June being the apparent key month is no doubt due to the fact that the greatest xylem formation takes place during this month. Total annual precipitation shows scarcely any correlation with the growth-ring curve, which indicates that it is the distribution of the rainfall which is of greatest importance. When one compares average growth of all the trees with average June precipitation for the years 1913, 1922, and 1930 it appears that there is a lag of one year in growth. The first conclusion one would be inclined to draw is that there must be an accumulative effect which tends to weaken the tree and consequently shows its effect in reduced growth in subsequent years. Although it is widely believed that xylem is largely formed at the expense of food manufactured during the current season and not from reserve material from the previous year, the writer knows of no conclusive evidence to this effect. It would be interesting to collect increment cores from a number of beech trees which have succumbed since 1930, in order to determine whether there was a gradual decrease in growth or whether normal growth continued up to the time of the death of the tree. It is, however, possible to explain this lag in growth without having to assume a reduced vitality in the tree. In referring to the weather summaries for the year in which a decreased growth took place, one finds that in these years there was an accumulated moisture deficiency in the soil from the previous year's drought. Quite possibly then, this lag in growth was due to the continued lack of available soil moisture. According to weather records, 1913 was a comparatively dry year in northern Indiana and in 1914 the month

of June was drier than usual. Weather summaries for 1922 indicate that rainfall was far below normal for that year and in 1923 there was a deficiency of ten per cent for the month of June. Here again it appears that a dry June following a drought year resulted in a decided decrease in wood formation. The decrease in growth in 1925 was due to some other reason because 1924 was a wet year. The weather records state that May and June of 1925 were extremely dry and hot, and this combined effect of heat and drought must have been responsible for the decreased growth the same year. Again referring to figure 2 for a comparison of precipitation and growth, it is evident that there has been a decided drop in both rainfall and growth since 1928. Although the recent drought is generally referred to as the 1930 drought, it really began in the early part of December, 1929 and in certain parts of the " Corn Belt," the ground water supplies have not yet returned to their previous levels. Most of the water from the meager rains and winter snows which seeped into the ground was taken up by the upper horizons of the soil and, as a result, there was a blanket of very dry soil between the upper horizons and the lowered water table. This condition still existed in many places in the spring of 1933. When one compares June precipitation of 1931 with the average annual ring width, there is a third example of the effect of a dry June following a drought year. Although precipitation was 0.93 inches above normal in the northern section in June, 1931, the month closed with the subsoil moisture still decidedly deficient in all sections of the state and streams were at their lowest levels since 1895. This again substantiates the theory that decreased growth was due to an accumulated deficiency of soil moisture from one season to the next.

### Average June Temperature and Width of Growth Rings

Ordinarily one would suspect that increased temperature would result in increased growth as the average temperature for May and June would hardly appear to be above the optimum for the fundamental processes, including photosynthesis, and its resultant effect on growth. However, increased temperature increases transpiration and consequently has the same ultimate effect as a decreased water supply. High temperature due to its effect upon transpiration would, where the water supply is a limiting factor, intensify the effect of low rainfall and partially nullify the beneficial effect of high rainfall. A low soil moisture supply coupled with high temperatures during the tree's greatest physiological activity is apparently very effective in limiting growth on account of the close relation which exists between turgidity and growth. In seasons of insufficient water supply, the reduced turgidity limits both the total leaf area and the total amount of sugar synthesized. Since temperature through its effect on transpiration influences the saturation deficit of the leaves the stomata of the leaves remain closed the greater part of the day when the water supply is critical, with the result that there is a reduced gas exchange capacity and a resultant decrease in food manufacture. This conclusion is strik-

ingly supported by the data and graphically portrayed in figure 2. On careful study of this figure, one finds a much more direct relation between the average width of growth rings and temperature than between growth and precipitation. Years showing high radial growth are correlated with low June temperatures and years showing decreased radial growth are correlated with high June temperatures. For example, the weather summary for June 1914 states that the mean temperature for the month, 75.0° was 3.7° F. higher than normal, and was the highest mean temperature on record for the month of June since 1890. The weather summary for June, 1915, a good growth year, indicates that the weather of the month was cool and in striking contrast with the excessively hot, dry weather experienced in June, 1914. For 1923, a poor growth year, the June summary states that in the northern division, the temperature was above 90° at practically every station every day from the 18–26th. Rainfall was deficient by 10 per cent. The following year was an excellent growth year and the weather records for June of this year read as follows, ". . . there was an unusually large number of days with rainfall in the first and third decades, precipitation occurring at many sections nearly every day. The percentage of sunshine naturally was much lower in the northern division where the rainfall was the heaviest." The year 1928 represents the maximum average annual growth for all trees for the 1913–1933 period. The weather record for June of this year further substantiates the conclusion that it is low temperature and high rainfall during June which make for rapid growth. The record states: " The outstanding features of the month were the unseasonably cool weather which prevailed throughout, and the excessive amounts and frequency of rainfall. It was the coldest June on record, with a deficiency of 5.8° F. Precipitation was generally above normal in all parts of the state. Only one year, 1902, has shown a higher June rainfall." Before the writer actually made measurements of the beech increment borings he expected 1930 to stand out as the minimum growth year of the 1913–1933 period. To his surprise the rings for 1931 and 1933 were much narrower than those formed in 1930. As mentioned before, there was an accumulated deficiency of soil moisture in June of 1931 following the 1930 drought. The heat wave during June merely intensified the effect of the drought in reducing growth. The increased growth in 1932 was again correlated with June temperature and precitation in that both factors were consistently near the normal. From figure 2, it is evident that 1933 shows the lowest average annual growth and the highest June temperature for the 1913–1933 period. The average temperature of 77.2° marks it as the warmest June of the 1887–1933 weather record for the state. With an average rainfall of only 1.16 inches, it was also the driest June since 1887. " No June in the climatological history of the state has had so few days with 0.01 inch or more of precipitation, and none so many clear or so few cloudy. The effect of heat and drought was generally unfavorable to crops and the month closed with marked deterioration evident in gardens and pastures."
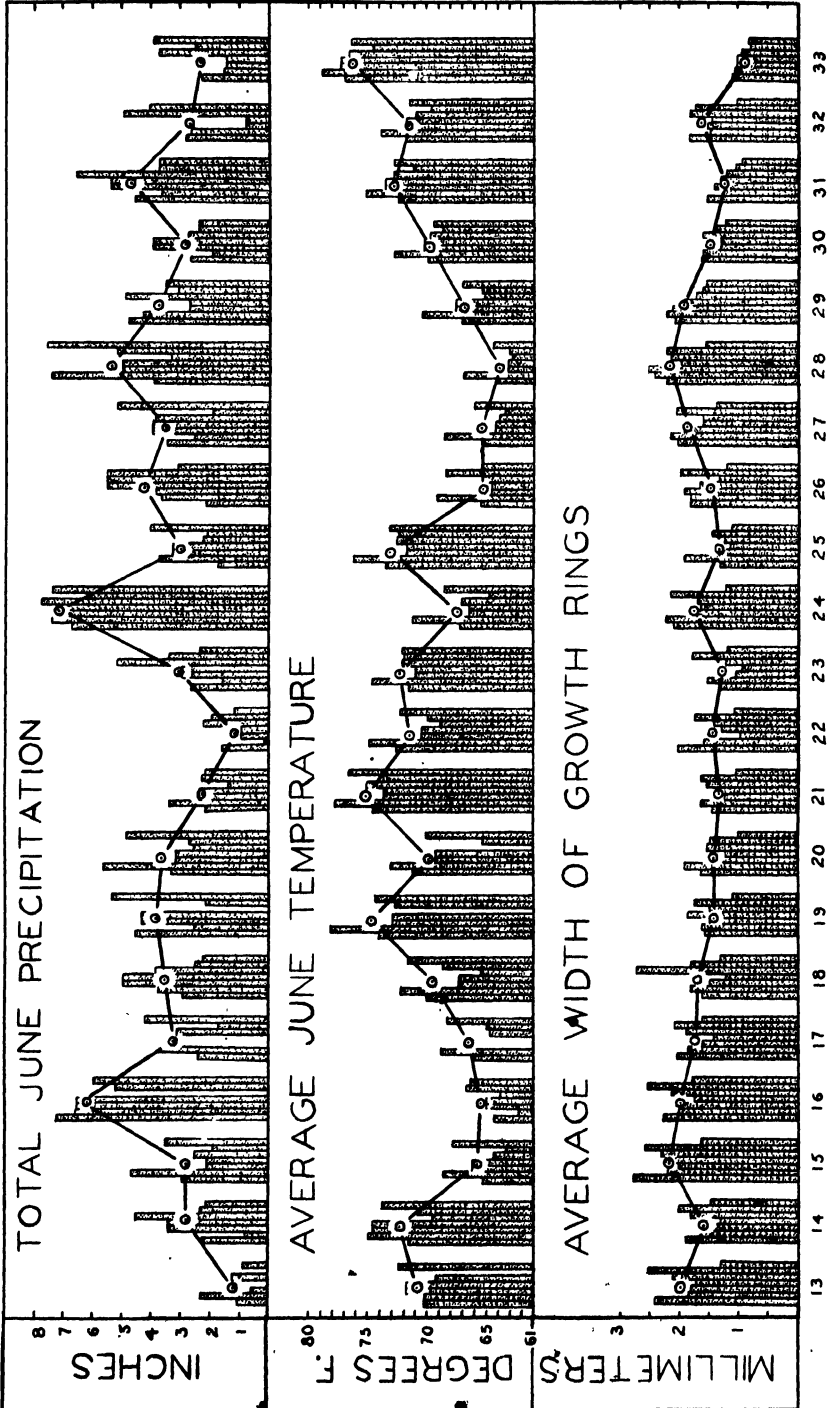
FIG. 2. The relation of growth of beech to temperature and precipitation for the years 1913–1933. Each column represents the average width of growth rings for 10 trees in each of 7 woodlands. The trend line represents the average width of rings for 70 trees. Each column represents the average precipitation or temperature for the station nearest the woodland studied.

It is these two factors of June temperature and precipitation which un-
doubtedly limit the western extension of the beech-maple forest type. If we
were to have an extended period of years with June weather conditions such
as occurred in 1928, the beech-maple forest type would undoubtedly advance
farther west, but with only a few consecutive seasons similar to June 1933
there would probably be a decided retrogression with the corresponding ad-
vance of the oak-maple and oak-hickory forests.

## CORRELATIONS

Figure 3 represents a statistical analysis of June rainfall and temperature
compared with the average annual growth of ten trees and the seven weather
stations nearest the woodlands studied. From the regression lines for width
of rings and precipitation, a fairly positive correlation is shown for the Swope
Woods but very little correlation is shown for the Berkey Woods and for the
average for all trees and all stations. As has been suggested before, drought
years usually show their effects on growth the following year probably due to
an accumulated deficiency in soil moisture, whereas wet years show an in-
crease in growth the same year. This consideration, together with the fact
that rainfall is an exceedingly variable factor throughout a given region, makes
it practically impossible to correlate statistically the relation between rainfall
and growth. Temperature, on the other hand does not show such wide local
variations as are exhibited by precipitation. The regression lines for growth
and temperature (fig. 3) show a very decided negative correlation between
temperature and growth. According to Fisher's tables giving significant
values of correlation coefficients, the value 0.526 indicates high significance
which further indicates the very high negative correlation shown between
growth and temperature in all three cases in figure 3.

It is recognized, of course, that other factors besides precipitation and
temperature influence growth of trees. Mineral salts, wind, intensity and
duration of light are of great importance. The precipitation records as ob-
tained from the weather stations are not the most satisfactory expression of
moisture relations. Soil moisture samples taken periodically from the vari-
ous horizons of the soil would be more satisfactory than precipitation records
because such factors as run-off and seepage would be eliminated. Also, evap-
oration data would be more desirable than average temperature data because
the factor of relative humidity would be taken into account. Until, however,
we perfect more refined methods of measuring these factors in the field it is
necessary to rely upon empirical methods which were used in this study.

## SUMMARY AND CONCLUSIONS

The average annual ring width for 10 dominant beech trees in each of
seven beech-maple woodlands of northern Indiana has been determined for
the period 1913–1933.
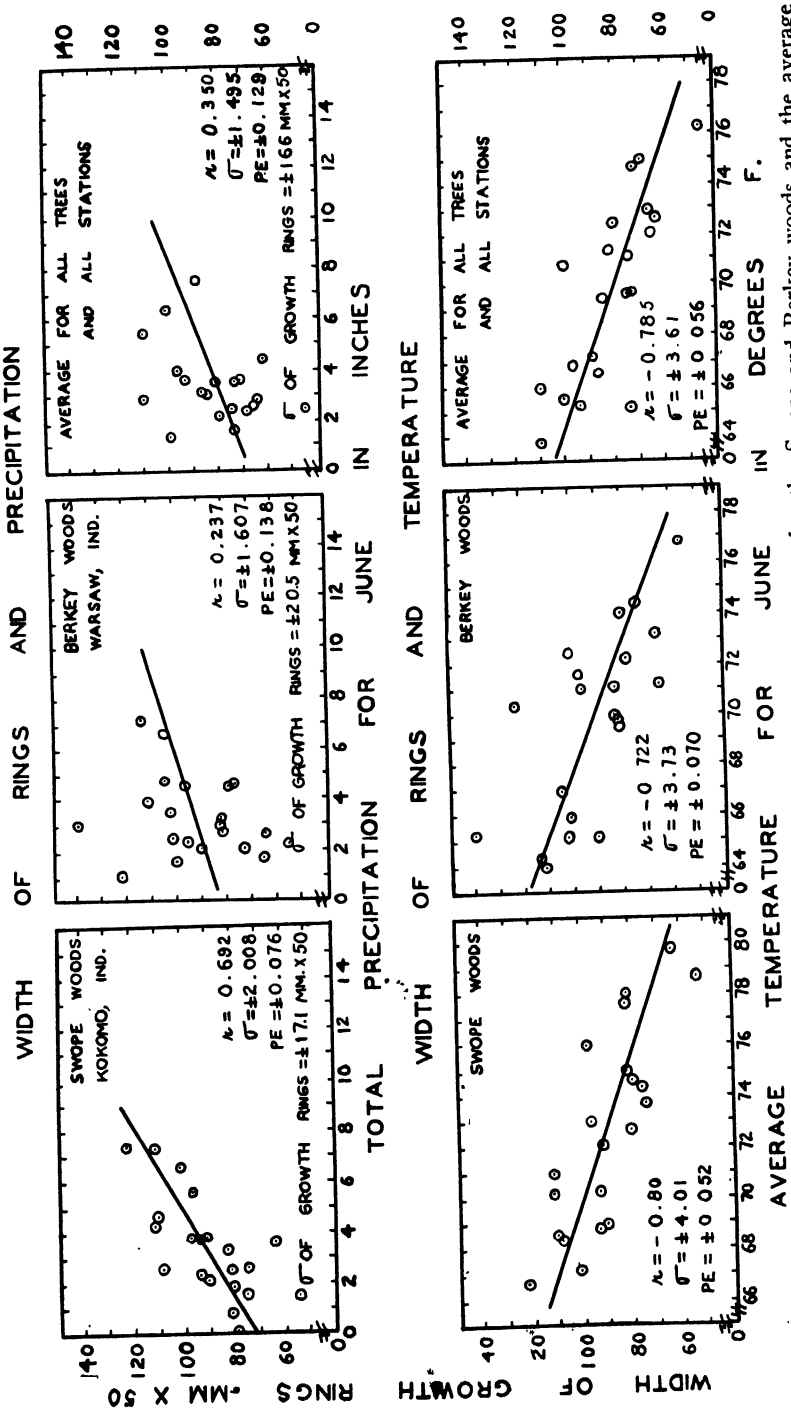
Fig. 3. Correlation of width of growth rings with precipitation and temperature for the Swope and Berkey woods and the average for all trees and all stations.

Yearly variations in the width of the annual rings for 1913-1933 are correlated inversely with the average temperature for the month of June.

Yearly variations in the width of the annual rings for 1913–1933 are correlated directly in certain woodlands with the total precipitation for the month of June at stations nearest the woodlands studied.

In most cases, drought years show their effects on growth the following year probably due to an accumulated deficiency in soil moisture, whereas wet years show an increase in growth the same year.

Should this period of drought years continue over an extended period, these data indicate that there would probably be a gradual retrogression of the beech-maple type with the corresponding advance of the oak-maple and oak-hickory forest types.

Since high temperatures and drought years have such a marked effect on the growth of mesic species such as beech, it appears advisable that in the reforestation program of the middle western states where these extremes occur to select more xeric tree species for planting.

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# ATTACHMENT OF LARVAE OF THE OLYMPIA OYSTER, OSTREA LURIDA, TO PLANE SURFACES

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It is characteristic of oyster larvae, as well as the larval forms of a great many fixed marine invertebrates, that they are free-swimming for a considerable length of time before becoming attached and assuming the adult form. Prytherch ('31, '34) has recently made a study of the process of attachment, or setting, of larvae of the oyster (*Ostrea virginica*) native to the Atlantic and Gulf coasts, and has called attention to certain factors influencing the larvae in the attachment stage. This author's experiments dealt in detail with the nature of the setting process and the mode of metamorphosis, and took into account the chemical conditions of the water with respect to their effect in initiating the setting reaction.

In the present experiments attempts were made to determine the abundance of larvae setting as influenced by certain physical factors, without considering the original cause of setting. Growers and observers of the native oyster of the Pacific coast have commonly noted that a large proportion of the small oysters, or spat, are found on the under surfaces of shells or other material to which the larvae become attached. The question therefore arose as to whether this was due to some specific reaction of the mature larvae or merely to the fact that sedimentation and growth of algae and other organisms on the upper surfaces prevented attachment of larvae.

## MATERIAL AND METHODS

The species of oyster studied was *Ostrea lurida*, the native oyster of the Pacific coast, most commonly known as the Olympia oyster. This is a hermaphroditic and viviparous species, and the larvae are carried for some days within the mantle chamber before they are discharged into the open water.

The points to be made clear were, in the first place, whether larvae actually set most abundantly on under surfaces when upper surfaces are equally clean, and secondly, if so, what the reaction is which is responsible for such behavior. Frames were made of galvanized hardware cloth of ½ inch mesh, each frame holding three 8 x 10 inch panes of clear window glass one inch apart and parallel. These frames could be wired together so as to hold the glass plates at any desired angle.

Counts of spat were made also on a recently developed type of spat col-

lector. This is made of cardboard and is a modification of the standard egg crate filler so that its natural position in the water maintains some of the surfaces in a horizontal position while the others are vertical, and it permits the water to flow through the openings across the surfaces. These collectors are coated with concrete which is allowed to cure before they are placed on the oyster grounds.

## COUNTS OF SPAT CAUGHT ON SPECIAL COLLECTORS

Some of the spat collectors above described were left on an oyster bed for about three months before they were removed, broken apart, and the horizontal and vertical pieces segregated. Counts were made of the number of oysters on the vertical, upper horizontal, and lower horizontal surfaces. The area of each piece, considered as a plane, was measured with a planimeter.

TABLE I. *Number of spat counted on surfaces of concrete-coated cardboard spat collector left in water for about three months*

| Surface | Area cm.$^2$ | No. of Spat | No. of Spat per 1000 cm.$^2$ |
|---|---|---|---|
| Lower Horizontal | 1081 | 3497 | 3235 |
| Vertical | 1156 | 1232 | 1066 |
| Upper Horizontal | 1002 | 28 | 28 |

The results are presented in table I. About 115 times as many spat were on the lower as on the upper horizontal surfaces, and about three times as many on the former as on the vertical surfaces. Since the surfaces were in the water for about three months the result does not necessarily prove that the larvae actually set on them in these proportions, but might indicate the number of spat surviving without regard to the number originally caught.

## LIGHT AS AN ORIENTAL FACTOR

From the preceding account one draws the suggestion that the presence of most of the spat on under surfaces is due to a tropistic reaction to light whereby the larvae are directed into the shade. If this is the case it would appear to indicate, also, that attachment of larvae occurs almost entirely during daylight.

Fifteen glass plates were painted black on the upper surfaces and supported in frames. Similar frames supporting clear glass were prepared. All were placed on an oyster bed in a horizontal position and left for about 24 hours, during which short time sedimentation did not occur sufficiently to prevent light passing through the clear glass. After drying the plates the spat were counted on the under surfaces.

On the lower surfaces of the black glass 435 spat were counted, while on similar surfaces of the clear glass 616 were caught. That more larvae

became attached to the clear glass is not considered significant, but the experiment shows definitely that they do not attach to under surfaces because of a negative phototropic reaction.

### SETTING ON GLASS PLATES AT KNOWN ANGLES

In order to determine the relative number of spat actually setting on surfaces held at different angles, wire frames containing glass plates were placed on an oyster ground where they were completely covered with water even at low tide, and left for only one complete day. Thirty horizontal plates, representing 2400 square inches of under surface and the same area of upper surface, 30 plates in the vertical position, and the same number· held at an angle of 45° were placed in the water at low tide one day and left until the following day at low tide, a period of 24½ hours. During this time little silt or slime could collect on upper surfaces, and all surfaces may be considered as approximately equally clean. The factor of interference with attachment of larvae due to unclean surfaces was thus eliminated. All frames were placed within an area of a few square yards and the results may be expected to be comparable. Fifteen of the plates held at an angle of 45° and an equal number of those fixed at 90° were placed so that the general tidal flow was parallel to the surfaces, while the other 15 plates of each group were roughly perpendicular to the direction of flow.

TABLE II. *Number of spat caught on plane glass surfaces as determined by the angle of the surfaces. See text and figure 1*

| Angle of Surface | Area Sq. In. | No. Spat | Av. No. Spat per 2400 Sq. In. |
|---|---|---|---|
| 0° | 2400 | 1195 | 1195 |
| 45°[1] | 1200 | 42 | 181 |
| 45°[2] | 1200 | 139 | |
| 90°[1] | 2400 | 6 | 11 |
| 90°[2] | 2400 | 16 | |
| 135°[1] | 1200 | 1 | 3 |
| 135°[2] | 1200 | 2 | |
| 180° | 2400 | 1 | 1 |

[1] Perpendicular, [2] parallel to general direction of current.

After removal the plates were allowed to dry and the number of spat on all surfaces carefully counted. The results are given in table II. . The under horizontal surfaces are considered as having an angle of 0°, while the upper surfaces of the same plates are 180°. The under surfaces of the diagonal plates are treated as 45° and the upper surfaces as 135°. Both surfaces of the vertical plates are recorded as 90°, and the area of 90° surface was therefore twice as great as that representing any other angle. When these results are plotted graphically (fig. 1) it becomes clear that there is a close correlation between the angle of the surface and the number of spat caught. It will be noted in table II that the 45° and 90° plates which were parallel to the direc-

tion of tidal flow caught definitely more spat than those perpendicular to the direction of the current.   Clearly this is owing to the fact that in the former case more larvae-bearing water passes over the surfaces.   In a sense it would furnish a more accurate description of setting behavior to plot the frequency of attachment on those plates parallel to the direction of the current, rather than the average as in figure 1 which represents the distribution of spat under
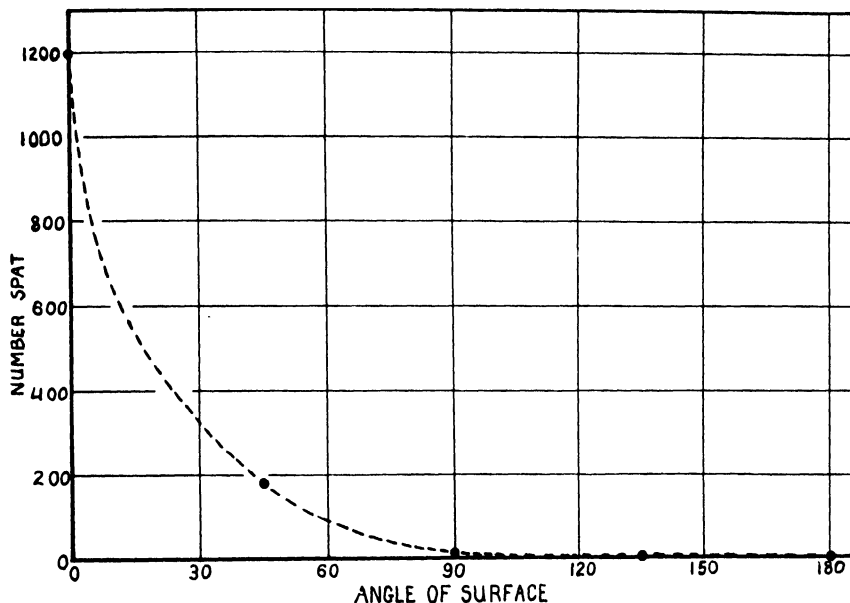


Fig. 1.   Graph showing number of spat caught (24½ hours) on surfaces (2400 sq. inches) held at different angles.   See table II and text.

natural conditions.   However, to do so would not change the curve significantly, as may be seen by comparing with table II.   The results with the 45° and 90° plates are in accord with expectations after noting the great difference between the frequency of attachment to lower and upper horizontal surfaces, where the mechanical effects of the current are practically identical.

The effectiveness of the surface increases directly as it approaches an angle of 0°, constituting the under horizontal surface.   The values form a relatively smooth hyperbolic curve.   The results indicate that the frequency of attachment as determined by the angle of the surface is due to some definite mode of behavior of the larvae, and not to mechanical effect of some of the plates on the current.

## DISCUSSION

It has been demonstrated above that the larvae of *Ostrea lurida* set primarily on under surfaces, and that the frequency of attachment is greatest when the surface is horizontal.   On plane glass about 100 times as many spat

were caught on under horizontal as on vertical surfaces, while almost none attached to upper horizontal surfaces. It was demonstrated further that this is not due to a negatively phototropic reaction.

The possibility that the larvae may be negatively geotropic suggests itself. It is probable, at least, that the mode of setting is due to gravity, though a tropistic reaction may not be concerned. It appears most likely that the explanation of these results lies in the swimming position of the larvae. Hori ('33) carried on experiments with this species whereby he kept the larvae in tanks until they attached. He wrote (pp. 273–275), "After the renewal of the water the larvae swam about very actively and floated to the surface in a mass, with their velum upward."

The foot, by means of which the larva holds on to a surface before cementing itself, is adjacent to the velum at the open borders of the valves. The velum is a rather flattened, ciliated swimming organ and must support the weight of the body proper and the larval valves. In this case the velum would naturally be maintained above the body, and the foot would be pointing upward. As one watches the larvae swimming in a dish it is noticeable that they characteristically swim in this position, though swaying back and forth. Presumably in nature, as the larvae are carried along with the current, the foot may cling to a surface with which it comes into contact. This, most frequently, would be an under surface, and the more nearly horizontal the surface the more likely the contact. If this explanation is correct it may be considered that the above-described habit of setting, while due to the effect of gravity, is not due to an actual geotropic reaction.

It may appear superficially that there is some contradiction in the results of the tests with the concrete-coated collectors and those with the glass plates. In the former case the under horizontal surfaces bore about 3 times as many spat as the vertical surfaces, while in the case of the glass panes about 100 times as many caught on the lower as on the vertical surfaces. The difference is obviously owing to the fact that while the glass furnished plane surfaces the spat collector consisted of highly irregular surfaces. The vertical walls of the collector, due to the roughness of the cement-sand mixture with which they were coated, have a large horizontal component in the projecting sand grains. Therefore, in this case, no surface was either totally horizontal or vertical with respect to the oyster larvae, for the larvae are considerably smaller than the grains of sand. It is most likely also that stereotropism plays a significant part in the attachment of larvae to rough surfaces. Ordinarily spat are found most abundantly in the crevices and minor depressions of shells. A reliable comparison of the exact effectiveness of different planes is furnished only by the tests with the glass plates.

If the above-described explanation of the habit of attachment to under surfaces is correct it would be expected that in places where the water is highly turbulent the larvae would frequently be turned over and would become attached to upper surfaces also. This may readily be observed on oyster

grounds near Olympia, Wash., where the water flows rapidly over dikes. Besides the dikes shells and rocks bear oysters on the upper surfaces as well as the lower, while away from the dikes they are almost entirely on under surfaces.

## SUMMARY

Spat of the Olympia oyster, *Ostrea lurida,* characteristically are found most abundantly on under surfaces of shells, etc.

This is due, not to the possibility that survival on such surfaces is greatest, but to the fact that the larvae actually attach most abundantly to lower surfaces.

By employing plane glass plates it was found that more than 6 times as many larvae attach to under horizontal surfaces as to the under surfaces of glass supported at an angle of 45°, and about 100 times as many as caught on vertical surfaces.

A curve is plotted to show the hyperbolic relationship between the number of larvae attaching and the angle of the surface.

This behavior is apparently not due to a tropistic reaction to light but most probably to the swimming position of the larva whereby it is commonly maintained in the water with the foot upward.

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# A STUDY OF SITE, ROOT DEVELOPMENT, AND TRANSPIRA-
## TION IN RELATION TO THE DISTRIBUTION
## OF PINUS CONTORTA

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### Introduction

It has long been known that under certain conditions lodgepole pine, *Pinus contorta* Douglas, is the first coniferous invader of areas denuded by fire. There are little more than casual observations as to what are the specific limiting factors. Rigg and Harrar ('31) report it occurring in western Washington in sphagnum bogs, in light gravelly soils, and in light soils overlaying lava flows. Joseph Howell ('31) says, " In the western yellow pine, *Pinus ponderosa*, stands of California, there are to be found groups of lodgepole pine. It is obvious to a careful observer that these stands are not the result of fires, but are due to some soil condition—a condition not conducive to the growth and development of western yellow pine, but favorable to lodgepole pine."

Howell studied essentially level ground where he found the *Pinus contorta* consocies in small, slightly depressed areas, usually about six inches below the general level of the land. These depressions, he found, were underlaid by a clay " hard-pan " which was impervious to moisture and caused the formation of a perched water table.

Interest in this problem arose through our observation that lodgepole pine is never found on the southwest (Moscow) side of Thatuna Ridge, while immediately upon crossing the summit to the north or east, it occurs quite commonly in flats and on protected slopes. It is found in hollows, gulches, and on north and east slopes, all areas protected from the southwest wind, which is the prevailing one in this region.

In these localities the surface layer of the soil is underlaid by a " false hard-pan " formed by the deposition of colloidal material leached from the surface soil. This hard-pan is so resistant to roots as to greatly distort them. It is not impervious to water, but owing to its highly colloidal nature has a high water-holding capacity, which results in the raising of the level of the water table.

The senior writer has observed *P. contorta* growing in western Montana, Wyoming and throughout the length of Idaho; always where the force of the wind was somewhat reduced.

It occurs along Pack River north of Sandpoint, Idaho, in depressions

between the knolls of the slightly undulating valley floor where the soil is light and sandy, and of the same texture to a depth of at least six feet. The water-retaining capacity of this soil is very limited, and for this reason the presence of the tree was not at first understood. However, the fact that the region gets about 40 inches of rainfall annually in comparison to the 21 inches received at Moscow, coupled with the probability of subirrigation from the river, seemed to explain satisfactorily the presence of the pine under these conditions.

P. contorta was found in the Clearwater National Forest near the Cool Water lookout station on an exposure where the protection from southwest winds was not immediately evident. A study of the surrounding country revealed that higher mountain ranges some miles distant did protect this area to some extent from the strongest air currents. The spot was, however, subjected to considerable wind. The altitude here being between six and seven thousand feet, the winters are long and the snowfall heavy. This, combined with frequent summer showers, results in the soil being well supplied with moisture during practically the whole growing season, in spite of the desiccating effect of some wind.

## Field Work

Suspecting that the root system of this pine might in some way limit its distribution, we dug a number of young trees from typical sites, endeavoring to select trees growing under identical conditions and of approximately the same age. The root systems of not only *Pinus contorta*, but also of *P. ponderosa*, *Pseudotsuga taxifolia*, and *Larix occidentalis* were studied. These are the trees most frequently found competing with lodgepole pine. The latter has a rather short taproot, and the main laterals diverge from it comparatively near the surface of the soil, while the uppermost laterals of *P. ponderosa* and of the other species studied diverge from the taproot at a greater depth, and are more evenly distributed throughout the remaining length of the taproot. Also, the lateral roots of *P. contorta* were found to extend in a somewhat horizontal direction slightly beneath the surface of the soil, while those of *P. ponderosa* grew more diagonally downward, and penetrated to greater depths.

The following detailed report of the field work done on Pack River is representative. Two lodgepole pines, each about eleven years old, and one ponderosa pine were excavated. A circular trench with a radius great enough to include most of the laterals was dug around each tree. The soil about the roots was then dislodged, the dirt removed, and the trench deepened. This process was repeated until as much as possible of the root system was exposed. In general appearance there was a marked similarity between the root systems of the two. The larger laterals in both cases originated within an inch of the surface of the soil, and extended almost horizontally outward for an average

distance of 23 inches. The laterals originating at a depth of slightly more than 4 inches below the soil's surface were short, small, and few in number.

Ponderosa pine was very rare in the vicinity of this lodgepole stand. The only specimen found growing under conditions comparable to those of the majority of the *P. contorta* was 19 years old. Notwithstanding its greater age, the general aspect of the root system of this tree resembled very closely that of much younger members of the species excavated in other localities. Haasis ('21) reports, "*Pinus ponderosa* is marked by a very constant general type; a main vertical root with a number of laterals of different lengths and variously placed."

The ponderosa taproot was excavated to a depth of 58 inches; and it was one-half inch in diameter at the point at which it was severed. The main lateral roots branched from the taproot within the first 21 inches below the surface of the soil, and from the point of origin grew more obliquely downward than did the lodgepole laterals. Distribution of laterals was noticeably more uniform throughout the length of the taproot of *P. ponderosa* than of *P. contorta*.

## Experimental Work; Methods and Materials

For the study of the effect of soil aeration on root and shoot development, seedlings of both species were grown in six different groups, aerated by different methods and to different degrees. The soil for these cultures was taken from both *P. contorta* consocies and *P. ponderosa* consociations. In collecting the soil, the duff was removed from areas considered typical, the underlying 8 inches of soil taken to the greenhouse, screened through a 2 mm. mesh sieve and used to fill eight-inch earthen flower pots, some of which were provided with aerators.

The aerators consisted of a 10 mm. glass tube, closed at one end, as a central axis, to which were attached three sets of cross arms 6 mm. in diameter, and so arranged as to afford six separate and equally distributed outlets (fig. 1). They were placed in the pots with the outlets about one inch from



Fig. 1. An aerator for pot cultures.

the walls of the pot. To the base of the central tube, extending through the bottom of the pot, was attached a rubber tube, the free end of which was connected with the air hose of an automobile pump when the soils were to be aerated.

The first five groups were planted on December 19, 1931, and the sixth on January 8, 1932. When the seedlings appeared to be established all were
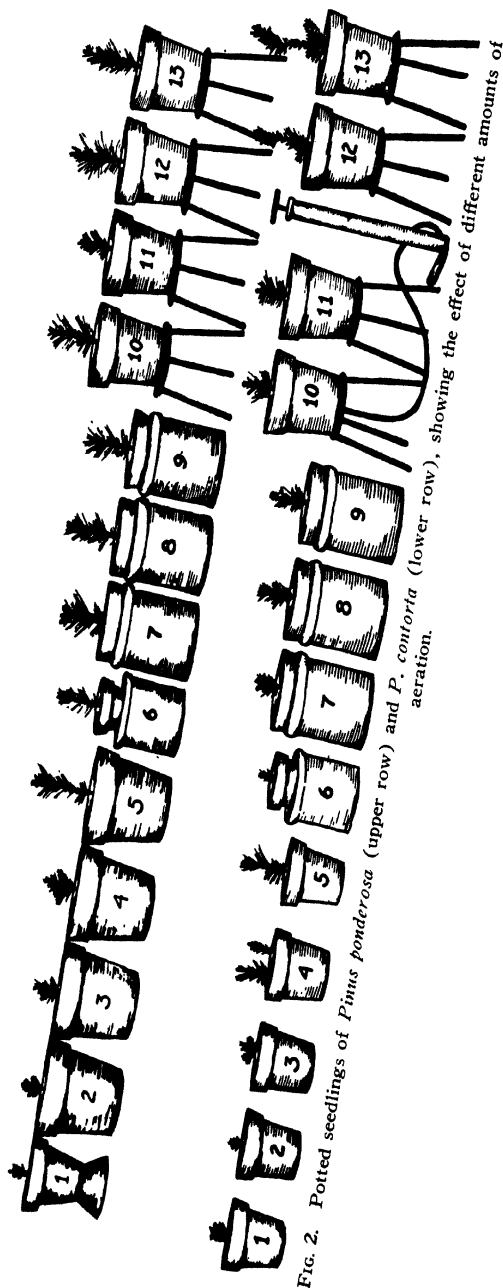
Fig. 2. Potted seedlings of *Pinus ponderosa* (upper row) and *P. contorta* (lower row), showing the effect of different amounts of aeration.

removed except a single one in each pot. All seedlings were removed from the pots on the same day, when the oldest were approximately six months old, the soil carefully washed away and measurements of root and shoot made for all individuals.

## PROCEDURE AND RESULTS

### Group 1.   Numbers 1 in Figures 2, 3, and 4

The seedlings of this group were grown in pots completely coated with a paraffin-beeswax mixture, with stoppered drainage openings, and containing soil from a *P. ponderosa* consociation. As soon as a seedling had appeared in each pot, the soil was covered with water and kept in that condition for the duration of the experiment. Though general development of both species was more inhibited in this than in any other group, there was a very noticeable difference in response of roots, presumably to oxygen deficiency. The ponderosa pines had the characteristic relatively long taproot, but with very few, rather short laterals sparsely distributed along its length. All submerged organs of this species were soft and spongy, and hypertrophy was evident, especially at the base of the stem (no. 1, fig. 4).

The roots of the lodgepole pines appeared to be normal in texture and showed no hypertrophy; but the taproot was very short and bore a large number of much branched laterals, which were close to the soil's surface (no. 1, fig. 3).

### Group 2.   Numbers 2 in Figures 2, 3, and 4

The seedlings of this group were also grown in stoppered and waxed pots, the only possible access of air being through the surface of the soil, which was from a ponderosa pine consociation. Instead of being saturated, these were given barely enough water to secure germination and limited growth. General development was better for both species in this group than in the preceding one. While the taproots were of about equal length, the distribution of the laterals on the taproot was much more uniform in *P. ponderosa* than in *P. contorta*.

### Group 3.   Numbers 3, 4, and 5 in Figure 2; Numbers 3 in Figures 3 and 4

Half the number of seedlings of each species were grown in soil from a *P. ponderosa* consociation, and the remainder in that from the *P. contorta* consocies. The pots used were neither waxed nor stoppered, and the soil was kept moist. Aeration was through the soil surface, water added, and possibly to a limited extent through the porous walls of the pot. Development, especially of tops, was much better for both species in this group than in the two previously discussed. The lateral roots, here too, diverge from the taproot at higher levels in the lodgepole than in the ponderosa pine (figs. 3 and 4).
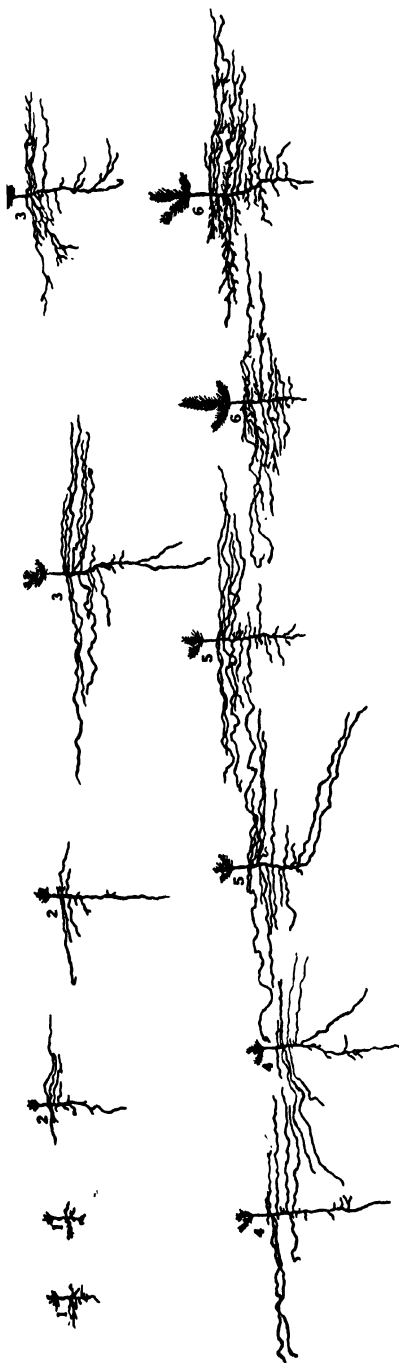
Fig. 3. Root systems of *Pinus contorta* seedlings showing responses to different degrees of soil aeration.
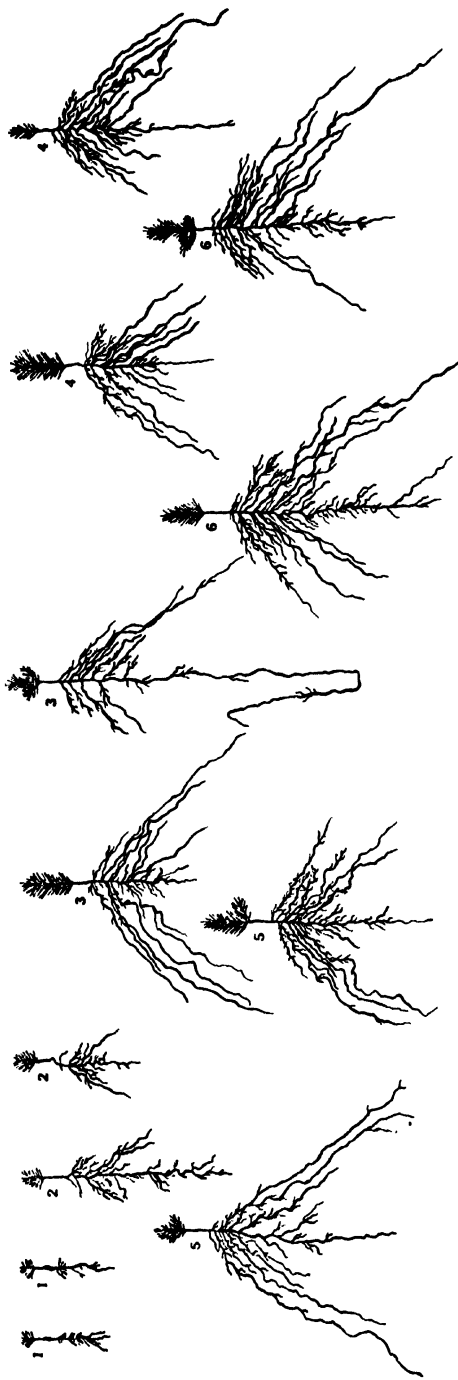
Fig. 4. Root systems of *Pinus ponderosa* seedlings showing responses to different degrees of soil aeration.

*Group 4.    Numbers 6, 7, 8, and 9 in Figure 2; Numbers 4 in Figures 3 and 4*

The pots used were neither waxed nor stoppered, and were selected for size and shape so that when set in glazed earthen crocks the bands around the tops of the pots rested on the rims of the crocks. The seedlings being given more water than the soil would retain, the excess was collected in the crocks below and was used for watering the seedlings the following day. The passage of water through the soil served as the aerating device. In this group, too, half the seedlings of each species were grown in *P. ponderosa* soil, and the remaining ones in *P. contorta* soil.

The lodgepole pines of this group attained about the same general level of development as those of the preceding group, but that of the ponderosa seedlings was noticeably better. The tops of the latter species had twice the number of branches, and the length of tap and lateral roots was much greater than for group 3 (figs. 3 and 4).

*Group 5.    Numbers 10 and 11 in Figure 2; Numbers 5 in Figures 3 and 4*

The seedlings of this group were grown in pots, half of them containing *P. ponderosa* soil, and the rest *P. contorta* soil, and all of them equipped with the aerators previously described. They were given an optimum supply of moisture and aerated under pressure by ten strokes of the automobile pump once daily. The lodgepole pines were much sturdier and healthier in appearance, and their roots had more branches and greater total length of laterals than those of any previously discussed group (no. 5, fig. 3). The distribution of laterals on the taproots more nearly approached that of the ponderosa pines than before, but they were still limited to higher soil strata. The ponderosa pines failed to make quite the development of those aerated by an excess of water.

*Group 6.    Numbers 12 and 13 in Figure 2; Numbers 6 in Figures 3 and 4*

These seedlings were planted 28 days later than those of group 5, half of each species in *P. contorta* soil and half in ponderosa soil, in pots equipped with aerators. They were aerated by 20 strokes of the pump—ten twice daily. In these cultures both species outstripped in top growth the older plants grown under all other conditions, including those aerated by 10 strokes of the pump per day. The root system of *P. contorta* was definitely better developed in this than in any other group, and more nearly equaled that of *P. ponderosa* in extensiveness and distribution of laterals under these conditions. However, the general relationship between the root systems of the two species held through all six groups, that is, ponderosa pine always had a longer taproot with more evenly distributed laterals than did the lodgepole.

Other conditions being constant, there appeared to be no consistent difference in development of either species whether grown in soil from a *P. ponderosa* consociation or that from a *P. contorta* consocies.

TABLE I. *Comparative Development of Roots and Shoots as Effected by Different Methods of Aeration. Measurements in Centimeters*

| Planted December 19, 1931 | | *Pinus contorta* | *Pinus ponderosa* |
|---|---|---|---|
| GROUP I Pots waxed. Soil saturated. | Average height of shoots | 2.33 | 4.13 |
| | Average no. of branches per plant | 0.00 | 0.00 |
| | Average limits of distribution of main laterals as measured from soil surface | 1.13–2.38 | 3.00–4.00 |
| | Average no. of lateral roots per plant | 19.00 | 4.00 |
| | Average total length of laterals per plant | 29.00 | 24.00 |
| | Average length of taproots | 6.00 | 13.00 |
| GROUP II Pots waxed. Minimum water content. | Average height of shoots | 4.00 | 6.16 |
| | Average no. of branches per plant | 0.00 | 0.50 |
| | Average limits of distribution of main laterals as measured from soil surface | 2.00–14.25 | 3.83–23.5 |
| | Average no. of lateral roots per plant | 47.00 | 56.00 |
| | Average total length of laterals per plant | 161.00 | 188.00 |
| | Average length of taproots | 30.33 | 31.00 |
| GROUP III Pots not waxed. Optimum water content. | Average height of shoots | 8.33 | 9.80 |
| | Average no. of branches per plant | 0.66 | 1.30 |
| | Average limits of distribution of main laterals as measured from soil surface | 1.62–11.00 | 2.81–30.50 |
| | Average no. of lateral roots per plant | 41.00 | 60.87 |
| | Average total length of laterals per plant | 112.00 | 240.34 |
| | Average length of taproots | 34.83 | 39.50 |
| GROUP IV Aerated by an excess of water. | Average height of shoots | 7.25 | 10.00 |
| | Average no. of branches per plant | 1.25 | 3.50 |
| | Average limits of distribution of main laterals as measured from soil surface | 1.46–6.21 | 2.92–14.00 |
| | Average no. of lateral roots per plant | 67.00 | 44.00 |
| | Average total length of laterals per plant | 193.00 | 477.00 |
| | Average length of taproots | 29.25 | 63.25 |
| GROUP V Aerated by 10 strokes of pump. | Average height of shoots | 6.66 | 10.00 |
| | Average no. of branches per plant | 2.50 | 2.00 |
| | Average limits of distribution of main laterals as measured from soil surface | 1.58–12.83 | 3.25–17.75 |
| | Average no. of lateral roots per plant | 59.66 | 33.00 |
| | Average total length of laterals per plant | 286.50 | 407.00 |
| | Average length of taproots | 20.83 | 36.00 |
| Planted January 8, 1932 | | | |
| GROUP VI Aerated by 20 strokes of pump. | Average height of shoots | 11.75 | 13.66. |
| | Average no. of branches per plant | 4.25 | 5.00 |
| | Average limits of distribution of main laterals as measured from soil surface | 2.10–14.20 | 3.14–21.33 |
| | Average no. of lateral roots per plant | 46.50 | 49.33 |
| | Average total length of laterals per plant | 338.00 | 398.00 |
| | Average length of taproots. | 23.25 | 42.66 |

In table I are given the average values, for the two species in each group, of the measurements made on all the individual seedlings included in the experiment.

## EFFECT OF WIND

To determine the effect of wind, 28 *Pinus contorta* seeds and 28 *P. ponderosa* seeds were planted in alternate rows of two flats. The rows were two inches apart, and the individuals in the rows were separated by a distance of two inches; thus the two species were alternated under the same conditions. The soil used was identical in source and preparation to that previously described.

One of these flats was subjected for 12 hours each day to an artificial wind created by an electric fan and having a velocity of 22 miles per hour. The other flat was placed under identical conditions except that it was not subjected to wind. Each flat received the same amount of water. One month after planting, 14 seedlings of ponderosa and 11 of lodgepole pine had appeared in the control flat. In the flat subjected to wind 7 *P. ponderosa* seeds had germinated, but none of the *P. contorta*. The flats were kept under the same conditions for two months without any further germination.

## TRANSPIRATION STUDIES

For investigation of the relative rate of water loss of the two species, during the first week of August, 1933, a number of pot cultures of the two pines were planted in the same manner as those numbered 10–13 in figure 2 and aerated by ten strokes of the pump once daily. On April 25, 1934, when the seedlings were approximately 8 months old, the soil containing the small trees was dislodged from each pot, the roots carefully washed free of soil, and the seedlings immediately placed in small bottles of tap water fitted with corks. A hole 5 mm. in diameter had been bored through the center of each cork, and a lateral incision, from the outside of the cork to the hole, made down one side. The stems of the seedlings were wrapped with cotton, the corks spread, then closed about the stems, pressed firmly into the necks of the bottles and sealed with the mixture of paraffin and beeswax. When the preparation had hardened, a fine needle was thrust through the outer shell down into the cotton surrounding the stem. This treatment permitted the slow entrance of air to replace the water transpired.

As soon as the plants had been treated in this manner, each bottle and contained seedling was weighed on an analytical balance and the weight recorded. Ten individuals of each species were placed under an electric fan and the remaining 20 plants were placed in as nearly identical conditions as possible, except that they were in still air. The velocity of the wind produced by the fan was about 22 miles per hour.

The average circumference of leaves taken from the top to the bottom of representative seedlings, and including every size, was determined for each species. Sections were taken from the base to the tip of these leaves, and with a calibrated microscope, the diameter of 100 sections of each species was measured in microns.

The transpiration experiment extended over 54 hours, when the plants with their containers were again weighed. The water lost by each individual was calculated by subtracting the final from the initial weight of each system. After the final weights of all the bottles and contained seedlings had been determined, the seedlings were removed one at a time from their bottles, and each leaf cut off at its base. When all the leaves had been removed from one seedling, the root system and the stem were placed in a numbered weighing-bottle. The leaves were assorted, as far as seemed practical, into groups of four to ten that were of the same length. These were counted, their lengths measured in millimeters, and placed in the same weighing-bottle with the roots and stems from which they came. The weighing-bottle containing the entire seedling was then weighed on an analytical balance. When all the seedlings had been treated in this manner, they were placed in a Freas electric oven and dehydrated for 48 hours at a temperature of 105° C. They were then removed from the oven, cooled in a desiccator, and again weighed.

In table II are summarized the experimental results judged most important. The values presented in this table were determined by averaging the corresponding values for all the individuals of each of the four groups into which the plants were divided.

TABLE II.   *Averaged values of water loss from Pinus contorta and Pinus ponderosa in still air and when subjected to wind*

| | Sq. dm. leaf area per gm. dry weight | Gms. H₂O lost per gm. dry weight | Gms. H₂O lost per gm. fresh weight | Gms. H₂O lost per sq. dm. leaf area | % increase in water-loss in wind over that in still air on basis of leaf area |
|---|---|---|---|---|---|
| *P. ponderosa* in still air.... | 0.9270 | 11.53 | 3.56 | 12.31 | |
| *P. ponderosa* in wind.... | 0.7692 | 13.86 | 5.25 | 14.63 | 18.85 |
| *P. contorta* in still air..... | 1.4780 | 9.26 | 2.35 | 6.71 | |
| *P. contorta* in wind....... | 1.0910 | 11.87 | 4.36 | 11.74 | 74.98 |

The most striking fact brought to light by these figures is that wind of the velocity used, caused a percentage gain in water loss per unit leaf area for *P. contorta* of over four times that for *P. ponderosa.* Contrary to expectations, the rate of water loss for lodgepole pine in still air, whether computed on dry weight, fresh weight, or transpiring area, failed to exceed the corresponding value for ponderosa pine, being noticeably less in all cases.

The average number of square decimeters of leaf surface for the 20 lodgepole pine seedlings was 1.2845, and for ponderosa pine, only 0.8481. The larger value for *P. contorta* is due partially to the fact that the seedlings of that species were just beginning to branch and were thickly clustered with young leaves, while only a few of the ponderosa plants were branched at all, and their leaves were uniformly more sparsely distributed than were those of

the lodgepole pines. This fact, too, would tend to decrease the leaf area per unit weight for the former species. However, greater leaf area per unit weight seems to be a characteristic of *P. contorta* in the seedling stage.

## DISCUSSION

The combined results of these experiments seem to explain adequately the general limitation of lodgepole pine to areas largely protected from prevailing winds, as well as the ability of *P. ponderosa* to exist in very much exposed conditions. Whether the trees studied were seedlings from pot cultures grown under widely varying conditions, or older individuals from a naturally selected habitat, *P. contorta* was always found to have a root system that necessarily limited its absorption zone to a level much nearer the soil's surface than that of *P. ponderosa*. The latter species has a longer taproot with longer laterals divergent at lower levels (table I) and leading rather obliquely downward from their point of origin (fig. 4). The *P. contorta* laterals tend to maintain in their growth a position more nearly paralleling the surface of the soil. Such a root habit would be of great benefit to a tree growing in sphagnum bogs, where Rigg and Harrar ('31) report finding *P. contorta,* or over perched water tables, as Howell ('31) observed it in California. In either case only roots near the surface could, without difficulty, absorb enough oxygen to maintain life.

The lodgepole seedling grown in saturated soil (no. 1, fig. 3), with its profusely branched laterals clustered near the level of the soil surface, shows how well adapted is this species to such conditions. The ponderosa seedling grown under the same conditions (no. 1, fig. 4) demonstrates just as convincingly its lack of suitability to such a habitat. The few short laterals developed would possibly be inadequate for mechanical support, and certainly, distributed as they were and being soft, spongy, hypertrophied, and totally without root hairs they could not have been very efficient organs of absorption, especially of gases. Their appearance and texture led the observers to believe that death and complete disintegration of these organs was only a matter of time.

On the other hand, lodgepole pine is at great disadvantage in locations exposed to much wind, which tends always to desiccate most the surface soil upon which this species so largely relies for its supply of water and dissolved nutrients, as well as to increase the transpiration rate of this tree to a very much greater degree than it does that of ponderosa pine. Moreover, such localities are often subject to stronger sunlight and consequent higher temperatures in tissues of inhabitants, which Roeser ('32) has found to be a factor capable of increasing the rate of water loss much more in lodgepole than in ponderosa pine. The deeper and more extensive root system, and the much more uniform rate of water loss of the latter species make it comparatively well fitted to such conditions. If *P. contorta* is to survive in a habitat exposed to much wind, which it rarely does, it must have an abundant and comparatively constant moisture supply.

There are at least two possible explanations of the hypertrophy developed by *P. ponderosa* in saturated soil. Devaux ('00) in his experiments with a number of dicotyledons found that supplying abundant water to absorbing surfaces, and the reduction of transpiration were both followed by lenticel hypertrophy. He concluded that either or both treatments resulted in increased sap pressure, which was directly responsible for the rupture of affected cells. Under the conditions of our transpiration experiment the rate of water loss of lodgepole pine seems to have been less than that of the ponderosa trees. In saturated soil the rate of water absorption for the former species, with its seemingly more efficient absorbing organs, could scarcely have been less than that of the latter. While it is entirely possible that higher sap pressures did exist in ponderosa than in lodgepole pine, consideration only of the probable transpiration and absorption rates for the two species would indicate greater pressures within the latter. Nevertheless, no hypertrophy occurred in the lodgepole pines. Devaux's explanation does not seem to fit readily the requirements of this case.

The possibility that the limited amount of available oxygen is in some way responsible for this hypertrophy naturally suggests itself. Assuming this to be the cause, the failure of the lodgepole pine to develop this condition could possibly be explained by its adaptation for securing aeration when grown in saturated soil. While the writers feel that more experimental work is necessary for conclusive evidence, they consider the small amounts of oxygen in very wet soils a factor in causing hypertrophy, occurring under such conditions, worthy of further experimentation.

Roeser ('32), in his investigation on heat injury to *Pinus ponderosa, Pinus contorta, Pseudotsuga taxifolia*, and *Picea engelmanni*, found that the rate of transpiration of *P. contorta* increased very rapidly as the temperature was raised to 116° F. He concluded that the transpiration rate of ponderosa pine was, in general, more constant than that of any other species included in his researches. The results of the experiment on water loss as affected by wind tend to substantiate this conclusion. Roeser also stated that the rate of water loss was generally higher for lodgepole than for ponderosa pine. In view of the typical *P. contorta* habitat, one might well expect a more profuse use of water by that species. However, from the data given in table II, it would seem that the rate of water loss is greater for *P. ponderosa* when both species are transpiring in a quiet atmosphere, and at a normal temperature. The discrepancy in this result for the two experiments may be due to lack of uniformity of conditions such as rate of air movement, temperature, and relative humidity.

## SUMMARY

The lateral roots of *Pinus ponderosa* were inhibited when seedlings were grown in saturated soil, possibly because of the effect of the low oxygen content of such soil.

The submerged organs of *Pinus ponderosa* grown in saturated soil developed hypertrophy which was especially evident at about the junction of the root and stem, just below the water level.

The tap root of the seedlings of *Pinus contorta* grown in saturated soil appeared inhibited, but there were many short, stubby laterals just below the surface of the water. This would seem to be an adaptation to oxygen deficiency.

*Pinus contorta* has a shallower absorbing system and less extensive laterals than has *Pinus ponderosa*.

The transpiration rate of *Pinus contorta* was increased by wind much more than was that of *Pinus ponderosa*.

The transpiration rate of *Pinus contorta* failed to equal that of *Pinus ponderosa* when both species were in a quiet atmosphere.

The usual limitation of *Pinus contorta* to protected sites appears to be due to its shallower and less extensive root system, and to the excessive increase in its rate of transpiration when subjected to wind.

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# THE SEASONAL LIFE HISTORY OF AN AMPHIBIOUS SNAIL, *FOSSARIA MODICELLA,* LIVING ON SANDSTONE CLIFFS [1]

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In a recent publication, the writer (Van Cleave, '33) called attention to a peculiar adaptation of *Fossaria modicella* to an amphibious environment provided by seepage areas on essentially vertical sandstone cliffs of the Turkey Run State Park near Marshall, Indiana. For a number of years these colonies have been under observation and samples have been taken periodically in the hope of combining field observations with analysis of population samples to determine the seasonal life history of the species in this unusual amphibious habitat. The present study has extended over a period of three years, during which field observations and collections have been made by the writer as a holiday study in which all members of his family have cooperated. In taking samples, the only practicable method was found to be that of picking snails individually from the surface of the rocks and placing them in a vial of water. Given areas were gone over carefully to secure representative samples and in many instances when young snails were present the surface of the rocks was searched with a hand lens to avoid missing the smallest snails. Fortunately, the young snails lack the surface incrustation which tends to obscure the older snails, giving them the same color and appearance as the rock background.

Ten population samples have been preserved and subjected to statistical analysis, as shown in table I. Since all members of this genus are hermaphroditic, there been no complications in the interpretation of data due to sexual dimorphism and variable sex ratios which add difficulties to the interpretation of population samples in the Prosobranch snails (Van Cleave and Lederer, '33; Van Cleave, '34). All of the individuals represented in these samples have been measured. A vernier caliper was used for the larger snails and a calibrated ocular micrometer in a binocular microscope for the smallest individuals. On the basis of field observations, distribution curves, size ranges, and observations on living snails in the laboratory, a number of pertinent facts relating to the life history of the species have been determined.

Analysis of the data available at the present time makes it possible to interpret the following features of the life cycle of *Fossaria modicella* in the habitat under consideration: (1) the number of broods per year; (2) the length of the individual life span; (3) the continuous change in facies of

population samples correlated with seasonal progression and advance of the modes representing parent and offspring generations.

TABLE I. *Summary of population samples of Fossaria modicella taken from sandstone cliffs at Turkey Run State Park, showing especially the progressive change in upper and lower limits of shell height*

| Date of collection | Number of individuals | Graph no. | Size extremes in mm. of shell height | |
|---|---|---|---|---|
| | | | Minimum | Maximum |
| 17.III.34 | 85 | 1 | 1.38 | 7.58 |
| 2.IV.34 | 178 | | 1.58 | 7.05 |
| 8.IV.33 | 104 | | 2.74 | 7.26 |
| 22.IV.34 | 229 | 2 | 1.79 | 8.00 |
| 15.VI.34 | 355 | 3 | 2.11 | 7.79 |
| 9.VII.32 | 50 | 4 | 4.00 | 8.21 |
| 26.VIII.32 | 393 | 5 | 2.00 | 8.20 |
| 8.X.33 | 259 | | 2.74 | 8.42 |
| 29.X.33 | 123 | 6 | 2.74 | 8.63 |
| 1.I.34 | 17 | | 4.32 | 7.37 |
| Total ............. | 1793 | | | |

At the time when the original note on this habitat was published, no specimens of *Fossaria* had ever been found in the streams within the ravines nor in the pools near the foot of the cliffs. All of the early field observations had been taken during the summer months. Under dates of March 17 and April 2, 1934, melting snow and ice and recent rains had rather conspicuously altered conditions at the base of most of the sandstone cliffs. Shallow excavations and basins which are perfectly dry for most of the year were filled with standing water. Under these conditions, large numbers of *Fossaria modicella* were gathered from submerged portions of the rocks, but a careful search with a hand lens failed to reveal any of these water-dwelling snails on sticks or leaves in the same pools. The young, newly hatched, snails seemed to be more abundant immediately below. and at the water level than on any other part of the habitat. Larger specimens were not as abundant here as on the face of the rocks several feet above the water line in the same general location described in the preliminary report.. This observation would seem to give evidence that the newly hatched individuals of *Fossaria modicella* in the habitat under consideration have stronger tendencies toward aquatic existence than do the mature specimens. But even the young retain their relationship to the essentially vertical submerged rocks as evidenced by their failure to crawl onto other objects in the pools.

There is marked seasonal variation in the relative abundance of *Fossaria* on individual areas designated for study. This variation is in large measure correlated with relative amounts of surface moisture on the cliffs. Thus the population of the same area fluctuates widely from year to year and from season to season. Some moist areas which were heavily populated in March, 1934, were completely dry and devoid of snails in late April of the same year.

Similarly, some individual areas heavily populated in the wet season of 1933 were but scantily occupied on corresponding dates of 1934 when rainfall and groundwater were markedly reduced.

On January 1, 1934 and again on March 17, of the same year, opportunity was presented to observe the influence of ice on the exposed snails. On both of these dates most of the seepage areas were encrusted with masses of ice. In January, very small numbers of *Fossaria* were found even after careful and prolonged search. The snails were usually located on the rock surfaces at the edge of ice patches. When ice masses were pried loose from the face of the rocks and crevices in the sandstone were investigated, there were no evidences indicating a tendency for the snails to seek shelter or to secrete themselves. It is evident that the adverse conditions of winter materially reduce the population of *Fossaria*. With the onset of winter, there is apparently a rather marked falling off in numbers of large snails. However, this seems to be due to retardation of individual growth rate rather than to the elimination of the individuals which have already attained large size. As shown in table I, the maximum size attained by individuals in winter and early spring is distinctly below that of summer and fall months. Thus the attainment of a given maximum size is not strictly a specific character of this species for it is in great measure influenced by environmental factors.

TABLE II. *Tabular summary showing size distribution of individual collections of Fossaria modicella*

| Shell height in mm. | 17.III.34 | 2.IV.34 | 8.IV.33 | 22.IV.34 | 15.VI.34 | 9.VII.32 | 26.VIII.32 | 8.X.33 | 29.X.33 |
|---|---|---|---|---|---|---|---|---|---|
| 1.3–1.7 | 3 | 7 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 1.8–2.2 | 9 | 31 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| 2.3–2.7 | 22 | 29 | 1 | 13 | 3 | 0 | 8 | 1 | 1 |
| 2.8–3.2 | 9 | 29 | 4 | 19 | 40 | 0 | 15 | 12 | 5 |
| 3.3–3.7 | 9 | 21 | 5 | 27 | 59 | 0 | 31 | 21 | 8 |
| 3.8–4.2 | 5 | 9 | 2 | 31 | 30 | 3 | 40 | 35 | 9 |
| 4.3–4.7 | 4 | 16 | 18 | 34 | 65 | 2 | 57 | 53 | 19 |
| 4.8–5.2 | 8 | 11 | 27 | 43 | 51 | 11 | 65 | 40 | 28 |
| 5.3–5.7 | 9 | 14 | 27 | 24 | 54 | 8 | 76 | 35 | 22 |
| 5.8–6.2 | 3 | 1 | 10 | 22 | 35 | 12 | 57 | 14 | ·14 |
| 6.3–6.7 | 2 | 5 | 7 | 6 | 11 | 8 | 25 | 23 | 10 |
| 6.8–7.2 | 1 | 5 | 3 | 5 | 3 | 5 | 12 | 10 | 5 |
| 7.3–7.7 | 1 | 0 | 0 | 2 | 3 | 0 | 4 | 9 | 1 |
| 7.8–8.2 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 4 | 0 |
| 8.3–8.7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 |
| Totals .......... | 85 | 178 | 104 | 229 | 355 | 50 | 393 | 259 | 123 |

A study of the population samples summarized in tables I and II shows such definite seasonal variation in size of the individuals and composition of the sample, that much of the life history of the species may be reconstructed

by interpreting the evidences there set forth. In a total of 1793 individuals measured in this study, the largest shell was 8.63 mm. in height. This would indicate that the habitat under consideration is not especially favorable for the growth of *Fossaria modicella,* for in the literature (Baker, '11, p. 263) there are records of specimens of this species attaining a shell height of 12 mm. In the present study it has been found that there is a distinct tendency for shell height to follow a definite sequence of progressive increase in maximum size as shown in the last column of table I. Throughout the winter and early spring there is rarely an individual that is not distinctly below 8 mm. in height but individuals above that limit are fairly common in the summer and fall collections. By referring to the graphs it becomes noticeable that there is no season of the year when a cumulative effect is shown in the larger size group. This means that the individuals die soon after reaching the maximum size characteristic of the species and the season. If the attainment of maximum size were followed by a prolonged period of maintenance at a uniform size, the condition would be reflected in the distribution curves.

The progressive seasonal increase in size of the largest individuals through most of the year must be viewed as primarily a response to environmental conditions. However, this stands in sharpest contrast to the changing picture presented by the individuals representing the smallest snails. The two cyclic periods of progressive increase within the year are associated with the reproductive cycle and are therefore not directly correlated with environmental control of size. Each year two new generations appear, one in March and the other in late July or early August. At these times the minimum size range of shells drops conspicuously (table I) because a new cycle of egg production has brought forth a new generation of young. That these two periods are not the limits of a single prolonged period of egg laying is evidenced by the fact that no young shells under 4 mm. in height appear in any of the collections immediately preceding the advent of a new generation.

The smallest shells were found on March 17, when individuals 1.38 mm. in height were present on the cliffs. As the season progressed, individuals of the minimum size grew steadily in size until on July 9 the smallest young snails were 4 mm. high. Between July 9 and August 26 the smallest snails dropped from 4 mm. to 2 mm. Such a radical reduction in size following a consistent progressive increase through approximately four months can mean only one thing, namely, that a new generation has made its appearance. The writer was not as fortunate in being present for this event as he was for the March brood but the evidence indisputably places the time of the new generation between July 9 and the next collection on August 26. This deduction is supported by the fact that a few weathered egg masses were found still clinging to the rocks on August 26. The few weathered masses of gelatin were interpreted as representing the extreme end of a summer brood. Though this new generation fails to show as a separate mode on the graph in Figure 5

the recession of the minimum size at 4 mm. as shown in figure 4 to 2 mm. in figure 5 gives ample evidence of the introduction of a new generation into the picture.   The parent and offspring modes are clearly evident on figure 1 representing a March collection.   In this graph the mode for the new generation is at 2.5 mm. while that for the parent group is at 5.5 mm. of shell height.

At no season of the year have eggs been found in abundance but this fact is attributable to circumstances under which samples of the population were taken.   Had it been possible to visit the collecting sites more often there is little doubt but that eggs could have been found in abundance in the restricted periods of egg production.   A few masses were observed on August 26, 1932 and again on March 17, 1934.   On both of these dates the only egg masses discovered were on the face of the cliff a foot or more above the water level. On the last mentioned date, when young snails were especially abundant on the submerged rock face, particularly sharp attention was directed to the possibility of locating eggs in the pools, but with negative results.   The gelatinous egg masses on the exposed rocks become obscured by a flocculent yellowish material which seems to be an iron compound leached out by the seepage water.   Washing in water readily removed most of this material from the gelatinous mass making it much more easily distinguishable than when normally situated on the cliff.   For this reason it seems fairly certain that failure to find eggs in the water was not due to oversight since the masses would show up there more clearly than against the cliff face.

The question might well be raised as to whether the products of the two reproductive periods represent two distinct generations or two broods from the same parents as shown by Foster ('32) for the finger-nail shell, *Sphaerium solidulum*.   The available evidences seem to offer conclusive demonstration that there are two distinct generations per year, each of which produces but one set of eggs.   Graphs 1 and 2 represent two collections made in the spring of 1934.   Figure 1 indicates a population of *Fossaria* made up of a parent generation with a mode at 5.5 mm. shell height and a recently hatched offspring generation with a mode at 2.5 mm.   By April 22 (fig. 2), the mode for the new generation has advanced to 5 mm. and most of the parent generation has disappeared.   In some instances the growth rate of the new generation is so rapid that the distinct modes for parent and offspring groups are quickly obliterated.   Thus in figure 5, though the frequency curve is unimodal, field evidences and the absence of individuals below 4 mm. in height on July 9 (fig. 4) offer conclusive proof that a new generation is represented in figure 5.

Growth rate seems to be rather conspicuously different for the two broods of the same year.   In so far as present observations go, the individuals hatched in the summer brood never attain a shell height of 8 mm. while those of the spring brood reach as much as 8.63 mm. by fall.   This would seem to indicate that maximum size is not a naturally imposed limit in this species.

The normal life span seems to vary from approximately four to eight months for the individual in the habitat under consideration, but growth is so much conditioned by environmental factors that the older snails which live through the winter do not reach as great size as the spring brood most of which die off by late summer.
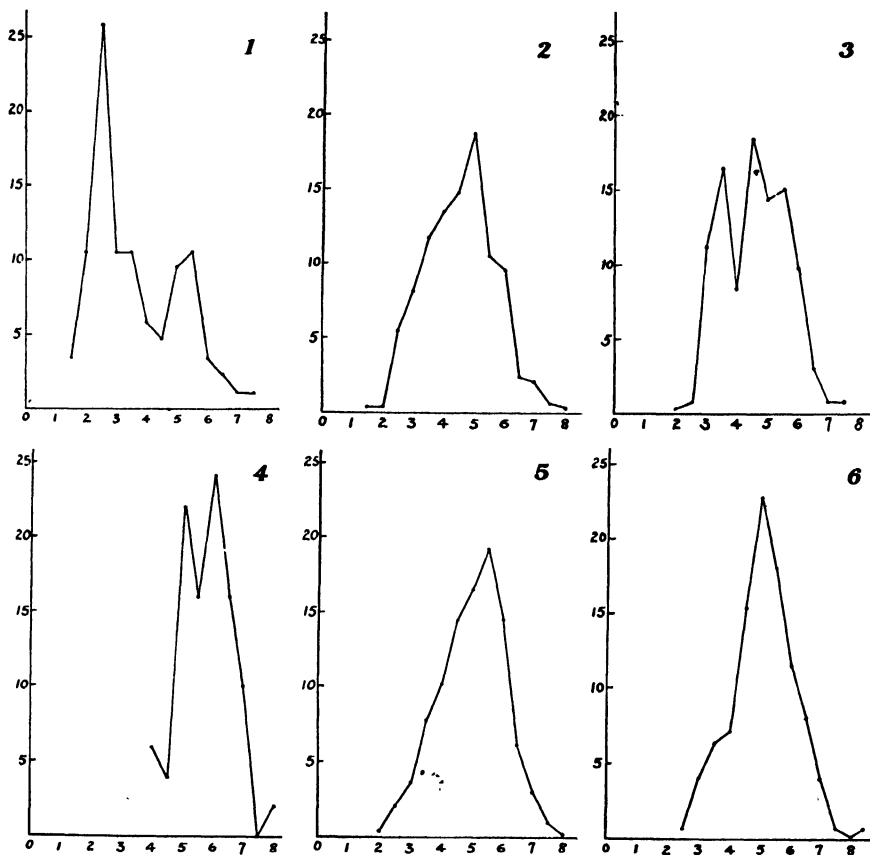


Graphs representing distribution in samples of *Fossaria modicella* drawn on a uniform scale. Abscissae represent shell height in increments of one-half millimeter. On the ordinate is plotted frequency in terms of percentage of the entire population sample of the date represented.

FIG. 1. Graph showing distribution of March 17, 1934. The mode at 5.5 represents the parent generation, that at 2.5 the newly produced spring generation.

FIG. 2. Population sample of April 22, 1934.

FIG. 3. Population sample of June 15, 1934.

FIG. 4. Population sample of July 9, 1932, just prior to the appearance of the summer generation.

FIG. 5. Population sample of August 26, 1932, a short time after the birth of the summer generation. Note drop in smallest group from 4 mm. in figure 4 to 2 mm. in figure 5.

FIG. 6. A typical fall sample.

The views on growth, expressed in the foregoing paragraphs, with reference especially to failure of the individual to maintain itself for some time at the maximum size level, are not in harmony with the general statements about size at maturity expressed in the literature on growth. In a posthumous volume on " Growth," Smith ('32, p. 19) advances the view that cessation of growth is distinctive of the adult period of life. Like most investigators who have studied the phenomena of growth, he draws his generalizations from the higher chordates. Among the vertebrates, Smith ('32, p. 23) recognizes that a normal adult size is not met with among the fishes for he states that in these " there is no stature associated with maturity which can be regarded as the normal stature." With regard to the other vertebrates he draws the conclusion (p. 19) that " During adult life the discharge of function is the dominant activity. Growth in stature has ceased." No one who has made an intensive study of any group of the invertebrates could subscribe to such a thesis. This concept implies an accumulation of individuals in the size group distinctive of the adult state. The extent of this cumulative effect would depend upon the relative length of life of the individuals after reaching maturity. The writer (Van Cleave, '34) and others, have shown that in a number of species of invertebrates, chiefly snails, the growth process is continuous throughout life, though of course much more rapid in the young, and that attainment of maximum size is at least in some species directly correlated with specifically imposed age limitations.

In *Fossaria modicella* it seems probable that age and environmental conditions more effectively limit growth than does attainment of maximal size. While there is apparently a specific limit to growth and to habitat variations in maximum size, actual size of the mature individual seems to be a resultant of two chief factors. Of these, growth rate is largely environmental, while length of life span seems to be chiefly independent of environmental influences and is probably hereditary, with seasonal influences probably playing a secondary rôle in determining the length of the life span.

## Summary

1. Field observations during three years and ten population samples have given information on the life cycle of *Fossaria modicella* living on sandstone cliffs.

2. A total of 1793 specimens have been measured.

3. There are two distinct broods per year, a spring generation in March and a summer generation in July or August.

4. Successive collections show gradual increase in size of the smallest individuals from 1.38 mm. shell height to 4 mm. There are two such cyclic progressions per year, correlated with the two generations.

5. Eggs have been discovered only on the dates when the smallest young were found.

6. Newly hatched individuals show a more markèd tendency toward

aquatic habit than older snails at periods of high water but even then they remain associated with the sandstone cliffs.

7. Seasonal influences on abundance and distribution are noted.

8. Individuals of the spring generation grow larger than those of the summer brood. The latter rarely reach 8 mm., a size very frequently attained by the spring generation.

9. Maximum size is not wholly inherited since it is influenced by environmental and seasonal factors.

10. Contrary to current generalizations on growth, individuals do not maintain themselves at a maximum size for a prolonged period after reaching maturity. Death comes with or soon after cessation of growth* for there is no cumulative effect in the group of large individuals.

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# REVIEWS

## THE HYDRATURE OF PLANTS [1]

This book, by one of Europe's leading plant physiologists, presents a new and interesting viewpoint of the rôle of water in plant life. The author's thesis is that inasmuch as water is intimately tied up with the physiological processes of growth, it is far more important that we consider this factor from a qualitative than from a quantitative standpoint. That is, we are not so much concerned with how much water is available to or used by the plant as we are with the condition of the water as found within the plant itself. To designate this so-called " water condition " (Wasserzustand), the author has coined the word " Hydratur," which by way of analogy may be said to be comparable to the word temperature which we commonly use to define the heat condition of the air. To quote the author's explanation of his concept of Hydratur:

" We are accustomed to differentiate between the *quantity* of heat, which is measured in calories and the *condition* of the heat, which we designate as its temperature. The biologist recognizes that in the physiological processes involved in growth the condition of the heat within an organism is of far greater importance than the total heat content. Something similar to this applies also with reference to the water content; though it should be understood that the relationships in regard to water are only mentally pictured as being similar to those pertaining to heat. But to explain why we should differentiate between quantity of water and its condition: the volume of water in a cell and the surrounding solution may be the same, but the *condition* of the water will be different if the vapor pressures in the cell and the solution are different. The relative vapor pressure can, therefore, serve as a measure of the condition of the water; for the designation of which the term Hydrature is proposed.

" For the proper physiological functioning of the plant organism the ' Hydrature ' of the cell plasma is of greatest importance. To determine the Hydrature one can use as an indicator thereof, the osmotic value of the cell sap, which always remains in equilibrium with that of the plasma. Thus, by virtue of this concept (of Hydrature) osmotic determinations of cell sap may be said to take on an entirely new meaning the significance of which had heretofore not been perceived."

On the basis of this concept of hydrature, Walter proceeds to point out the physiological and ecological significance of this " factor " in plant life. He warns the reader, however, against getting the impression that everything may be explained through the determination of the plant's hydrature.

[1] **Walter, Heinrich.** 1931. Die Hydratur der Pflanze und ihre Physiologisch-ökologische Bedeutung (Untersuchungen über den osmotischen Wert). 176 pp. 73 pl. 116 tables. *Gustav Fischer, Jena, Germany.* $4.00.

" Nothing could be less desired. The hydrature is merely a factor among many others. It undoubtedly plays a part in the physiological processes of all forms of plant life, but in very different degrees. While under desert conditions it is of outstanding significance, under conditions such as prevail in the moister mountain regions, this cannot be said to be the case. What significance it has under each individual condition cannot at the present time be stated with certainty but must await further investigation."

The book is divided into four parts. Part I deals with a general discussion of the concept of hydrature and its rôle in the life processes of the lower and higher plant forms; Part II deals in detail with the hydrature of the lower plants, namely, the molds, algae, mosses and ferns; Part III deals with the hydrature of the higher plants. Starting out with a discussion and criticism of different methods of determining cell sap density, Walter here calls attention to erroneous results and deductions made in the past due to faulty technique; then describes an improved method, as devised by himself, which is now quite generally accepted as a standard. This is followed by chapters on " The Hydrature of plants as an indicator of moisture conditions of the site," " The seasonal fluctuations of the Hydrature in different climatic zones," " The range of osmotic values of different plant types," " The determination of the minimum Hydrature and its significance," " The drought resistance and cold resistance of plants," " The Hydrature of the plant as a limiting factor in plant distribution," and lastly " The Hydrature of plants and the problem of adaptation." Part IV is an appendix of tables pertaining to osmotic values and relative vapor pressures of various acid and sugar solutions.

In the reviewer's opinion, the chief merit of Walter's book lies in the consistent treatment of the subject matter and the clearness with which the theories are expressed. To some it may appear that his discussions are too theoretical. That his deductions are, however, not merely fanciful theories, without foundation, is attested by the citation of numerous results based on field data collected by the author himself. Although the book should be of interest to all students of plant physiology and plant ecology, it should appeal especially to American workers in this field in that a major portion of it is based on data collected by the author during a year's sojourn in the United States. Especially interesting and perhaps the most convincing are the data and discussions pertaining to the Hydrature of plants indigenous to the desert regions of southern Arizona.

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## QUAIL IN ARIZONA

One of the pressing needs of present-day ecology is for more detailed studies of individual species, studies made in the field rather than on speci-

mens removed from their native habitat and placed under simulated natural conditions in the laboratory.

Gorsuch's recent paper [1] on the Gambel Quail is such a field study, and is the result of 3 years concentrated and accurate observation of the bird in its natural habitat. A careful reading of the publication leaves the reader with the feeling that the work is not only the effort of a scientist but of a naturalist as well.

Semi-popular in its presentation, the bulletin has an appeal and interest to the layman, yet because of its accurate scientific treatment is of equal interest to the scientist.

The author is endeavoring to put into practice methods for increasing the numbers of quail throughout their range. His suggested remedies relate in part to conservation of mature birds and in part to increasing their chances for propagation.

One of the best features of the publication is the detail given in most of the topics discussed. Outstanding examples of this are the sections on the food habits, the natural enemies, and the daily habits of the quail throughout the year.

A feature that renders the apparent purpose of the work less effective is the somewhat Utopian nature of some of the suggestions for replenishing the, at present, depleted numbers of the birds. The recommendation that over-grazing or even heavy though still correct utilization of the forage be discontinued in order to benefit the quail is not likely to be followed by the stockmen at whom it is directed, when it is considered that they have persisted in these practices in spite of the fact that by so doing they have in many cases lowered the carrying capacity of the range. For the same reason, the deferred and rotation grazing that is recommended is likely to meet with little or no sympathy on the part of the ranchers.

In the section on water, the conclusions that quail are able to live for long periods without free water, while very probably correct, is based upon too little evidence, some of which might even be construed as contradictory.

On the whole, the contribution is a valuable one to the knowledge of animal life in the southwest and it is to be sincerely hoped that the writer may not only continue this particular investigation but may extend his efforts to include other species.

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## RAUNKIAER'S ECOLOGICAL PAPERS

American ecologists owe much to the inspiration of the Scandinavian school. In spite of the handicap of its appearance in the Danish language, the epoch-making book by Warming in 1895 furnished the inspiration for the two

[1] Gorsuch, D. M. 1934. Life History of the Gambel Quail in Arizona. *Univ. Ariz. Biol. Sci. Bull. 2.* pp. 1–89.

branches of the American school of ecology that developed at the Universities of Chicago and Nebraska. While Warming may well be termed the father of modern ecology his successor at Copenhagen, C. Raunkiaer, soon became a leader in the quantitative study of plant communities. Again the handicap of a foreign language has prevented a great leader's contributions from being appreciated for their true worth. This should make the appearance in the English language of a complete collection of Raunkiaer's works [1] particularly welcome.

The translation of the Danish papers was done by H. Gilbert-Carter of Cambridge, and by Miss A. Fausbøll, while A. G. Tansley has translated three papers written in German and French. It seems likely that the uniformly excellent quality of the English is due to the careful editing of the whole volume by Tansley. A committee of Danish scientists had supervision of the task of collecting the manuscripts and the Rask-Oersted Fund contributed to the cost of publication.

Seventeen articles, chronologically arranged, are included in the volume, beginning with a preliminary paper on a classification of plants based on their adaptations to survive the unfavorable season. This appeared in 1904 and was followed in 1907 and 1908 by more complete discussions of these categories which soon became known as " Raunkiaer's life forms." This concept, together with its application as " Biological spectra " has proved useful in enabling phytogeographers to give more graphic descriptions of vegetation and in providing a phytogeographic characterization of the climates of the earth. It became somewhat familiar to American ecologists through the translations of Smith [2] and of Fuller and Bakke.[3] In its completed form it appeared in Raunkiaer's paper in German in 1918.

Raunkiaer's life forms now appear in many of the reports of European ecologists, and although rather tardily received in America, they have furnished the basis for several investigations, notably that of Ennis.[4]

Scarcely less notable than his life-forms and perhaps of even more significance in promoting the development of ecology have been Raunkiaer's methods of determining the degrees of frequency (valency) of the various members of plant communities. These methods were described in detail by Raunkiaer in a Danish paper in 1909 and in a French article dated 1918. They have had considerable acceptance in America and their accuracy and ad-

[1] **Raunkiaer, C.** The life forms of plants and statistical plant geography: being the collected papers of C. Raunkiaer. xvi + 632 *pp.* 189 *figs.* *Portrait.* *Oxford. The Clarendon Press.* $14.00.

[2] **Smith, Wm. G.** 1913. Raunkiaer's " life forms " and statistical methods. *Jour. Ecol.* 1: 16–26.

[3] **Fuller, Geo. D., and A. L. Bakke.** 1918. Raunkiaer's " life forms," " Leaf-size classes " and statistical methods. *Pl. World* 21: 25–63.

[4] **Ennis, Beulah.** 1928. The life forms of Connecticut plants and their significance in relation to climate. *Conn. State Geol. and Nat. Hist. Survey Bull.* 43: 1–100. 35 *figs.*

vantages have been discussed by McGinnies in a recent issue of this journal.[5]

When communities are investigated according to Raunkiaer's statistical methods the species composing them are found to have very different valencies or frequency indices. These species may then be segregated into various frequency classes and it has been found that the species with lowest frequency are decidedly the most numerous. This " Raunkiaer's law of frequency " constitutes another contribution by this leader. In America it has been applied and discussed by Kenoyer,[6] Gleason,[7] and others.

Included in this collection of papers are discussions of pioneer and arctic vegetation, of leaf size classes, of the influence of vegetation on soil acidity and of several minor ecological topics. More important, however, are Raunkiaer's botanical studies in the Mediterranean region, which occupy some 100 pages of the volume, one article of 75 pages now appearing for the first time. Special attention is here given to the life forms on the alluvial strand and on the sand dunes. Comparisons are made with the vegetation of similar situations in Denmark.

The size of the volume, the excellence of the typographical work, the abundance of the illustrations, the extensive bibliographies, and the carefully prepared index all go to make it the most important ecological book of the year.

<div style="text-align: right">GEORGE D. FULLER</div>

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<div style="text-align: center">ECOLOGICAL RELATIONS IN THE PITCH PINE PLAINS [1]</div>

Many thousands of acres in the midst of the Pine Barren area of southern New Jersey are occupied by a peculiar dwarfed vegetation of pitch pine with some scrub oak and minor shrubs, herbs, and cryptogams. The larger patches of this sort of vegetation are locally known as " Plains," and their rather unique aspect has led to considerable study with respect to their origin. Both unfavorable soil conditions and undue frequency of fires have been previously held responsible for the development of these plains, but there has never been a thorough study of the problem by modern ecological methods.

The paper before us presents the results of a carefully planned and skilfully carried out piece of ecological research. After preliminary reconnaisance, about forty stations were established for detailed investigation, half

[5] McGinnies, W. G. 1934. The relation between frequency index and abundance as applied to plant populations in a semiarid region. *Ecology* 15: 263–282. 4 *figs.*

[6] Kenoyer, Leslie A. 1927. A study of Raunkiaer's law of frequence. *Ecology* 8: 341–348.

[7] Gleason, H. A. 1929. The significance of Raunkiaer's law of frequency. *Ecology* 10: 406–408.

[1] Lutz, Harold J. 1934. Ecological relations in the pitch pine plains of southern New Jersey. *Yale University: School of Forestry Bull. No. 38.* x + 80 *pp.*. 18 *figs.*

in typical plains and half in surrounding areas. Numerous measurements were made of evaporation, soil moisture relations, and various physical and chemical soil features, but no difference between plains and pine barren communities sufficient to account for their contrasted vegetation could be discovered.

On looking into the situation with respect to fires results of greater significance were obtained. The Plains have been burned over on the average once in 8 years, the Pine Barrens once in 16 years. Considerable areas shown by historical evidence or by preserved stumps to have formerly been pine barrens are now plains, and on the other hand local protection has indicated the ability of pine barren to replace plains vegetation. The primary reason for the stunting of the trees on plains is, then, that shoots are destroyed by fire before they reach any considerable height, and so many sprouts arise from the stumps that any one is rarely able to develop normal tree stature.

Better fire protection is needed throughout the region. In the Pine Barrens this can be expected to result in more favorable tree form and in an increased number of the more desirable species of oak. If seedlings were permitted to develop in the Plains until large enough to withstand fire, vast areas could again produce useful timber. And if the litter were left to decompose naturally, the content of organic colloids in the soil of both communities might be increased, resulting in general soil improvement.

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A NEW BOOK ON ANIMAL BEHAVIOR [1]

It has been altogether too long since we have had a comprehensive summary of our knowledge concerning animal behavior. In the meantime information has accumulated and our point of view has shifted. The announcement of the present volume met a hearty welcome, the more so since English students have recently been doing an excellent job of producing readable and well balanced, brief summaries of various aspects of biology. Preliminary inspection indicated that this book would not be an exception.

The opening quotation from Professor Wheeler emphasizes the fundamental character of natural history and three of the nine chapters are devoted to interrelations of animal behavior and ecology with full and proper insistence that it is necessary to understand the natural relations between an animal and its environment before we are in a position to interpret its behavior. The attitude expressed in the preface that " the observer must be careful to state only the facts and avoid reading human motives, human ways of thought, into the behavior of his animal," is exactly as it should be.

Unfortunately the performance falls short of the promise. One might

[1] **Russell, E. S.** 1934. The Behaviour of Animals. An Introduction to its study. *London, Edward Arnold and Co.* 184 pp. $4.20.

explain away the continued use of such words as " bottom loving," " choice," " prefer " and " seek " as having been used on behalf of brevity and interest and being safeguarded by the attitude of objectivity professed in the preface. However, such kindly interpretations are severely tested by the following statement regarding a tortoise (p. 72) : " He had, like many of his kind, a passion for young peas. . . ."

Throughout the book, the author rejects the analytical method which attempts to split the situation or " perceptual field " into its constituent stimuli. Instead he emphasizes the necessity of using a so-called " direct method " which appears from the illustrations of dog, cat, wasp, and other complicated behavior complexes, to consist largely of describing the behavior of an animal as seen by an attentive observer with little or no attempt to control the environment. The casual-analytical method is relegated to the physical sciences and to physiology (p. 9) ; apparently the study of animal behavior is to be divorced even from the latter. The conditioned reflexes of Pavlov, the tropisms of Loeb or even of Kühn, and, by implication at least, the experimental analyses of Jennings, are all dismissed. Tropisms, in fact, are said to be, in the main, laboratory phenomena (p. 6).

The emphasis upon fitting the experimental situation to the possibilities of the animal is wholly excellent; however, the dismissal of controlled analytical experiments and concentration upon the supposedly simple " direct method " marks a scientific retreat. This is not a retreat from interpretation to observation as is suggested, but rather one from interpretation based on information from all possible sources to explanation based on extensive observations in natural and in relatively slightly modified environments. This is, at least in part, symptomatic of our age. Many agree with the author in not being content to allow the time needed for analytic exploration of the entire complex and are impatient of the sustained suspension of final judgment which is involved. Since the whole has not been so analyzed, the analyses that have been made are dismissed except where they demonstrate the inadequacy of present experimental methods.

As might be expected from this approach, the author is much interested in instinctive behavior and, in discussing instincts, draws heavily upon Hingston's uncritical writings. He accepts the relatively complex instincts· but strains at the equally innate but relatively simple tropisms. Is this because instincts have largely resisted analysis while tropisms have partially yielded to causal-mechanical attacks? The definition of an instinct (p. 96) lacks Wheeler's saving phrase (with an end or purpose of which the animal has no knowledge). Such an omission is to be expected from the general tone of the discussion foreshadowed (p. 3) by the statement that " Behavior is to a considerable extent determined by its result." This is not the place to examine carefully the fallacy in such philosophy. There is room only to suggest that life histories are selected as wholes as well as by parts and future

events in the life of any given individual are merely repetitions of many similar past events in the life histories of its ancestors.

The book is built upon the *gestalt* idea and is the expression of the philosophy of the organism-as-a-whole in an environment-as-a-whole rather than upon our information concerning animal behavior as a whole. In order to get his point of view accepted, the author is ready to sacrifice much that has been learned of behavior patterns together with all the accumulated evidence concerning the similarities between living and many non-living systems.

Despite these defects, this is a good book for a nature student who will recognize and correct for its limitations and prejudices. Oddly enough, it may be a good introductory book for some people in that it may stimulate their interest in animal behavior so that they may come in time to see the whole story. If however this is accepted as an adequate introduction to our present knowledge of behavior, the result would be as unfortunate as the similar acceptance of Loeb's summary in his *Forced Movements, Tropisms and Animal Conduct*. The book on animal behavior I have been hoping to see remains to be written; perhaps its preparation has been postponed and the difficulties of securing publication have probably been increased by the appearance of the present readable and superficially plausible account.

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## SYMBIOSIS BETWEEN ROACHES AND PROTOZOA [1]

As a sequel to his classical studies on the symbiosis between termites and their intestinal protozoa, Dr. Cleveland presents a comprehensive study of all phases of the interrelationships between an American wood-feeding roach, *Cryptocercus punctulatus* Scudder, and the protozoa found abundantly in its hind-gut. Twenty-five new species and eleven new genera of Hypermastigotes and Polymastigotes are described in great detail including a wealth of fine illustrations and careful cytological studies. In all cases, the families of protozoa coincide with those found in the termites and at the same time cover the range of variation found among the termite protozoa. One genus, *Trichonympha*, is abundantly represented in both the roach and in termites. Dr. Cleveland considers the evident relationships of roaches and termites as well as their protozoa as an indication of the ancestral symbiotic development, although it would seem to the reviewer that there is still a possibility that *Cryptocercus* might have picked up its protozoa from termites in later stages of its evolution. A more extensive world-wide study of the protozoa of wood-eating insects will ultimately throw more light on this problem. Dr. Cleveland has studied the allied roach, *Panesthia*, and finds it does not harbor cellulose-digesting protozoa, but rather has established a symbiotic relationship with cellulose-digesting bacteria in its fore-gut.

[1] Cleveland, L. R. 1934. The Wood-Feeding Roach *Cryptocercus*, Its Protozoa, and the Symbiosis Between Protozoa and Roach. *Mem. Amer. Acad. Arts & Sci.* 17 (2) : x + 185–342, 40 text figs., 60 plates (447 plate figs.).

*Cryptocercus* shows an interesting discontinuous distribution, localities from the Appalachian mountains and the Pacific northwest being the only records. Although classified as the same species, the Pacific form is somewhat larger and has one more molt in reaching maturity. Eighteen species of protozoa are found in both populations, while four species are found in the western form and not in the eastern form and three species are found in the eastern form and not in the western form. The distribution is limited by the necessity of moist logs, where the roaches are not subject to freezing temperatures, and relatively cool conditions in the summer, the cellulose-digesting protozoa having been shown to die in temperatures of 30° C. for twenty-four hours. It would seem difficult to find conditions which would join the western and eastern ranges of the roach later than the last interglacial period and the fact that there is so little divergence of the two protozoan populations indicates a relative stability of specific characters which is rather remarkable.

A series of ingenious experiments effectually demonstrate that many of the protozoa have cellulose-digesting enzymes within their bodies, that these enzymes are lacking in the tissues and fluids of the roach, that bacteria are not the main cellulose-digesting organisms, that dextrose is produced from the digestion of cellulose by the protozoa and that this sugar is then absorbed by the mid-gut of the termite. Striking adaptive mechanisms on the part of both the roach and its protozoa are described, the more outstanding adjustments being (1) a series of chitinous valves in the hind-gut which keep the protozoa confined to the colon except at the time of molting, (2) a large colonic sphincter muscle which forces the fluid from the hind-gut into the extraperitrophic space of the mid-gut but stops the passage of wood particles and protozoa, (3) a relatively impermeable peritrophic membrane extending through the mid-gut into the hind-gut which conducts the wood and protozoan cysts into the hind-gut without their coming into contact with the digestive epithelium, (4) the encystment or partial encystment of the protozoa during the molting period enabling individuals lacking protozoa to pick them up from fecal pellets, and (5) a perpetual colonial life rendered necessary through the fact that only molting roaches can bring about the infection of the young nymphs with the symbiotic protozoa. The adaptations, however, do not seem to be specific because the protozoa may be transfaunated from roach to termite and *vice versa*.

The reviewer is greatly impressed with the breadth of view, the thorough investigation of diverse but related problems, and the experimental techniques devised to test various hypotheses. Dr. Cleveland and his collaborators, S. R. Hall, Elizabeth P. Saunders and Jane Collier, are to be congratulated upon this memoir and the American Academy of Arts and Sciences upon its format and reproduction of the fine series of illustrations.

<div align="right">ALFRED E. EMERSON</div>

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# NOTES AND COMMENTS

## PRECIPITATION RETENTION BY CLADONIA MATS [1]

In the *Populus grandidentata* fire association of sandy, glacial soils in the northern portion of the southern peninsula of Michigan, the fruticose lichen, *Cladonia rangiferina*, quite frequently forms matted cushions in open, sunny places on the ground cover. During periods of moderate dryness these mats are gray, stiff, brittle, and transversed with shrinkage cracks; but after a rain the cracks disappear, and the mats become large and hummocky, green, elastic, and soft, due to the large amount of water absorbed. Allen ('29) showed that despite this large absorption of water, a ground cover of Cladonia is not favorable for the development of seedlings, because the mat prevents the roots of seedlings from coming in contact with the soil; swells on becoming wet, heaving the seeds and seedlings away from the soil; and " cracks " on exposure to the sun, the seedlings in the developing cracks drying up. Porter and Woollett ('29) proved by experiment that soil under the mat contains more moisture during dry periods than soil in the open; that soil under the mat does not receive as much moisture from rain and dew as soil in the open; and that the mat may absorb as much as 4.5 times its weight in water before allowing moisture to pass to the soil beneath.

It was to find an exact figure on the amount of precipitation retained by Cladonia mats before allowing moisture to pass to the soil beneath that this work was undertaken.

## METHODS AND RESULTS

The experimental apparatus consisted of five 8-inch U. S. Weather Bureau type funnels, each with a sieve soldered below the rim. On four a Cladonia mat of natural density was placed, the fifth being a control without such a mat. Each funnel drained into a separate container.

Artificial rains were produced with an ordinary garden hose.

Meteorologically, the summer of 1934 was normal, without drought, and with about an average rainfall, of both extremely light and more than moderate rains. During the period of experimentation (June 25 to August 15) there were 16 days of precipitation totaling 4.19 inches. In addition, 10 artificial rains produced a total of 3.73 inches of artificial precipitation.

As shown in the accompanying table, a Cladonia mat retains, on the average, 0.12 inches (extremes: 0.10–0.15) of precipitation, the differences being due, in part, to the intensity of the rains and the dryness of the mat just before a rain. Unless there is more than that amount of precipitation in any one rain, the soil beneath the mat does not receive any moisture, as was the case with one-third of the natural rains during the period of observation.

With artificial rains, however, the figure is somewhat greater, the mat retaining, on the average, 0.15 inches (extremes: 0.09–0.20) of precipitation.

[1] A contribution from the Biological Station of the University of Michigan, where the work was done under the direction of Professor Frank C. Gates, during the summer of 1934.

TABLE I. *Experimental data of precipitation and water retention by Cladonia mats. Measurements in inches*

| Date | In control | Under mat | Retained by mat |
|---|---|---|---|
| | Natural precipitation | | |
| June 25 | .01 | — | — |
| " 26 | .55 | .45 | .10 |
| " 28 | .02 | — | — |
| " 30 | .30 | .17 | .13 |
| July 6 | .51 | .38 | .13 |
| " 6 | .15 | .05 | .10 |
| " 10 | .19 | .05 | .14 |
| " 13 | .03 | — | — |
| " 13 | .13 | .02 | .11 |
| " 19 | .08 | — | — |
| " 21 | .09 | — | — |
| " 27 | .14 | .02 | .12 |
| " 29 | .53 | .38 | .15 |
| August 2 | .58 | .44 | .14 |
| " 8 | .60 | .47 | .13 |
| " 15 | .30 | .18 | .12 |
| Average [1] | .36 | .24 | .12 |
| | Artificial precipitation | | |
| July 4 | .41 | .27 | .14 |
| " 9 | .72 | .53 | .19 |
| " 12 | .44 | .27 | .17 |
| " 23 | .29 | .09 | .20 |
| " 24 | .60 | .45 | .15 |
| " 27 | .19 | .08 | .11 |
| " 31 | .24 | .13 | .11 |
| August 1 | .36 | .19 | .17 |
| " 3 | .19 | .10 | .09 |
| " 7 | .28 | .15 | .13 |
| Average | .37 | .22 | .15 |

[1] Includes only those rains in which water went through the mat.

## SUMMARY

By experimentation in northern lower Michigan during the summer of 1934 it was ascertained that all rains averaging less than 0.12 inches were retained by a normal *Cladonia rangiferina* mat.

Unless there was more than 0.12 inches of precipitation in any one rain, the soil beneath the mat did not receive any moisture, as was the case with one-third of the rains during that summer (a normal one).

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NOTE ON THE ENUMERATION OF INSECT POPULATIONS BY THE METHOD OF NET
COLLECTION

Our attention has been drawn by Mr. Geoffrey Beall at the Department of Applied
Statistics, University College, London, to the danger of misconstruction of a section of
our paper printed in Volume XIV, of ECOLOGY for October, 1933. It is hoped that this
note will serve to correct the error to which our wording in the penultimate paragraph
of page 364 at present lends itself.

One is frequently concerned not so much with the range of error to be expected be-
tween means, but with the maximum deviation due to sampling that an observed mean
is likely to show from the true value, or mean of the " supply " from which the samples
are drawn in a supposedly random manner. If $R$ be considered the maximum likely
range of error between the means of extreme samples, then the corresponding maximum
deviation, $D$, of those samples from the true value becomes $\frac{1}{2}R$ (assuming a reasonably
symmetrical distribution). The number of collections in the sample required to hold $R$
to a certain value is therefore 4 times greater than that required to hold $D$ to the *same*
value.

In our table V, the values of $n50\%$ and $n10\%$ are given as a solution of the range
of error problem. These values when divided by 4 will yield the number of collections
of 25 sweeps each which would be required in order to give reasonable assurance that
the mean of the collections did not deviate from the true value by more than 50% or
10%, respectively, of the true value. Or again, the values given in table V may be ap-
plied as a solution of the deviation from the true value problem by replacing $n50\%$ and
$n10\%$ by $n'25\%$ and $n'5\%$ respectively. Since the " degree of accuracy " of a mean would
generally be construed as referring to its deviation from the true value, the paragraph
following table V on p. 364 should be amended as follows:

> *Change* 10 per cent *on line 2 to* 5 per cent;
> *Change* 50 per cent *on line 4 to* 25 per cent.

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HAROLD E. GRAY

ENTOMOLOGICAL BRANCH, OTTAWA

WINTERING OF FIELD-LIVING NORWAY RATS IN SOUTH-CENTRAL WISCONSIN

In connection with the bob-white quail investigation carried on at the University of
Wisconsin from 1929 to 1932, observations were made on the wintering in the wild of the
Norway or barn rat (*Rattus norvegicus*). These observations may be looked upon as
typical for the south-central part of the state.

The summer rat population seemed sporadically distributed considerable distances
from buildings, notably in grain fields, along the shores of lakes and streams, and, of
course, about straw and manure piles, dumps, and abandoned farm buildings and corn
shocks.

After the cold weather shifting, that portion of the population still remaining away
from man's habitations appeared localized about particularly good sources of food. The
species was observed to persist along the shore of Lake Kegonsa quite late into the winter
of 1930–'31, living in holes in the banks and feeding upon dead fish, duck carcasses, and
other available animal matter. The bulk of the field-resident rats, however, stationed
themselves in the corn shocks left out in varying quantities throughout the area.

Field-wintering rat populations were never very dense, consisting in most instances
of two or three or a half dozen individuals occupying the corn shocks on a given farm.
Track trails in the snow seldom indicated the presence of more than one rat in a single
shock, and this was substantiated by the findings from shocks torn apart for examination.

As winter progressed, the rats of observational areas usually diminished steadily in numbers until by spring there would be practically no survivors about the shocks; indeed, save under exceptional circumstances, the whole out-of-doors away from buildings and used dumps could be said to be virtually rat-less at the end of the winter. Repopulation took place mainly through summer spread from buildings.

Owls and food shortage apparently constituted the major weaknesses in the winter equation of the field-living rats. The rats, even at remarkably low population densities, showed a peculiar vulnerability to the attacks of native owls. Owls as small as screech owls (*Otus asio*) took occasional individuals, and long-eared owls (*Asio wilsonianus*) have been noted to exert a highly disproportionate pressure upon the species.[1] The supreme enemy was the great horned owl (*Bubo virginianus*); unpublished as well as published data [2] revealed a pressure exceedingly severe in view of the comparatively insignificant numbers of rats commonly living in the wild.

On the basis of data from many thousands of owl pellet analyses, I would judge that native mammalian species anywhere near rat-like in size are scarcely represented in owl diets at all, if occurring in the wild at no greater than the usual rat population densities.

Dependence upon conveniently accessible and ample food resources, with consequent shortening of daily radii of movement, would itself place non-hibernating species at a decided disadvantage. A rat confined to one of two or three isolated corn shocks has not so many alternative courses of action in the event of emergencies. If an animal has or can find only one small habitat fit for it to live in, either it lives there or it doesn't live.

South-central Wisconsin furnishes field-wintering rats what looks like marginal environment at best, and it is not difficult to believe that the weight of owl depredations, plus those possibly of other enemies, is just enough to swing the balance completely against them. Doubtless, the rats accentuate their vulnerability of position through certain of their own specific habits. Running across the white snow surely exposes them to watchful predators. Their frequently noisy nocturnal behavior could hardly help attracting attention, and a hungry owl on a post would conceivably have plenty of time to await a rat the rustling of which it heard in a corn shock near by. And, too, a species, however adaptible and long successful against its ancient enemy, man, may not find racially new enemies easy to cope with.

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AGGREGATIONS OF *AMEIURUS NATALIS EREBENNUS* JORDAN, THE FLORIDA
FRESHWATER CATFISH

While driving westward on the Tamiami Trail out of Miami on May sixth, 1934, a remarkable series of aggregations of the Florida freshwater catfish, *Ameiurus natalis erebennus,* was observed.

A wide and deep canal parallels the highway, on its north side, and is connected at intervals of perhaps a mile with cross canals which pass under the highway, for the most part draining adjacent gladelands, but occasionally running on southwards for several miles.

At a bridge over one of these canals, approximately twenty-five miles from Miami, it was observed that the water of the main canal and the cross channel below the bridge was literally filled with catfish which were apparently between eighteen and thirty centimeters in length. These fish were first seen at about 7.45 A.M. Many were massed in

[1] **Errington, Paul L.** 1933. The long-eared owl as a ratter. *Condor* 35: 163.

[2] **Errington, Paul L.** 1932. Food habits of southern Wisconsin raptors. Part I—Owls. *Condor* 34: 176–186.

great numbers about several different centers, while others were swimming lazily about in all directions. Many garfish and other canal fish swam about among these catfish groups, near the surface, but the catfish were perhaps a hundred times more numerous.

Upon concentrating attention on these fish which were in the blind end of the channel, it could be seen that many of them had been severely bitten, probably by the garfish. Some were injured on the dorsal fins, while others were wounded or had bites taken from the caudal fin. No actual attacks were noted; even the injured fish swam past the garfish with no evidence of stimulation on the part of either species.

Fortunately one of two fish that were close to the bank was successfully taken in an insect net but the disturbance of the water by the splash of the net sent all the fish in that segment of the canal out of sight into deeper waer.

Such groupings of these fish were evident at several other bridges where there was little growth of *Nelumbo* and other water plants, but there was no opportunity to obtain additional specimens.

About 5:30 P.M. the catfish were still in very dense aggregations or groups near the surface, and the garfish still swam about between the aggregations. In one of the blind cross-channels having surface dimensions of perhaps twenty-five by forty feet, eight large groups ranging from three to four feet in diameter could be counted. It was impossible to judge the depth of each aggregation but if the depth approximated the surface measurements, the number of fish to each group must have been between three hundred and five hundred. For the most part all were massed with their heads in toward the center of the group, though there were many which merely maintained physical contact with other individuals on the outside of the aggregation.

At other cross channels and in the main canal, where there was no growth of water plants, these great aggregations were extremely numerous, with the fish tightly packed together, while smaller, more elongated masses in many cases connected the larger aggregations. A splash in the water, made with a stone in the hope of driving some individuals within reach of the bank, would break up the masses in that section of the canal, sending them at once to the bottom.

The specimen collected was a female, 19.5 cm. in total length. Inasmuch as its ovaries contained well-developed eggs, it seems probable that the aggregations witnessed were part of a behavior pattern connected with the breeding reaction.

Allee ('34), in summarizing Bowen's ('31-'32) work on the aggregations of juvenile *A. melas,* said: "With more extensive study of the aggregating behavior of the bullhead, *A. melas* by Bowen, . . . the importance of vision in the formation of aggregations of these fishes receives new emphasis. . . . Sight, the distance receptor, is re-enforced, perhaps by reaction to water vibrations produced by the tail of a passing fish, and on closer approach it is further re-enforced by contact reactions."

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### An Unusual Occurrence of the Convergent Lady Beetle

On the afternoon of September 1, 1934, the writer observed such an unusual number of the convergent lady beetle, *Hippodamia convergens* Guer., as to make it seem advisable to add this record to the literature on aggregations of lady beetles.

At the highest point of the north range of the Porcupine Mountains in Ontonagon County, Michigan, literally millions of these lady beetles were clustered on the bushes. They were clinging mainly to the stems of the plants from the surface to a height of three to four feet above the ground, and they also were found among the fallen leaves. On the main stems, they were four and five layers deep, completely covering the bark; on the side branches and leaves, they were less numerous. Practically all of the bushes on the summit of the ridge held thousands of the insects. The most common species of plants present were *Amelanchier* sp., *Pinus strobus, P. resinosa,* and *Quercus borealis,* all of which were less than ten feet in height. There was no species preference shown by the insects.

The ridge at this point is approximately 2,000 feet in elevation and about 1,400 feet above neighboring Lake Superior. It had been raining rather heavily the morning of September first and·the preceding day. The entire previous week had been cool with severe frosts at night. At the time of the observations, a brisk, cool wind was blowing from the southwest across Carp Lake valley, striking the ridge with considerable force. It was noted that on many of the more exposed plants the beetles were more numerous on the leeward side of the stems.

The beetles were quiet, there being very little movement in the masses on the stems or ground. They had apparently gathered in these enormous numbers preparatory to hibernation for the winter.

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# ECOLOGY

## SOME ANIMAL RELATIONS TO SOILS [1]

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The environment acts directly or indirectly on all living forms, modifying the general status of each individual. Plants and animals interact or coact with each other (Weaver and Clements, '29, p. 378). They also affect, or react on, their environment, more especially on soils and light.

Plant reactions on their environment are well known (Clements, '16, pp. 81–97), but animal influences have received much less attention, although their importance has been recognized since the time of Darwin.

With a widespread erosion control campaign actively going on throughout the United States looking toward better soil conservation than any we have ever had, and backed by the entire nation, it is peculiarly desirable to take full account of all important soils influences. Seemingly, soils specialists are giving more pointed attention to animals as part of the great soils complex. Let us examine or re-examine some of these animal effects.

(1) *Accumulating animal bodies or parts.*

The excreta, hairs, horns, skins, feathers, and other shed parts of animal bodies, and in the end, the bodies themselves entire, are continually being added to soils. On the Santa Rita Experimental Range (50,000 acres) the writer, on the basis of preliminary counts, has made a tentative estimate of the population and the weight of mammals belonging to two orders, namely the lagomorphs and the rodents, including the jack rabbits, cottontails, wood rats, kangaroo rats, pocket mice, ground squirrels, and grasshopper mice. The total numbers of all these creatures are estimated at 2,175,000 individuals, or 43 per acre; the total weight, at 438,436 lbs., or 8.7 lbs. per acre. But it is quite possible that these species make up but a small part of the weight of all the animals on the Range. Russell ('23, p. 14) records the approximate total

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weight of protozoa per acre of soil at Rothamsted at from 255 to 510 lbs., with the insects, nematodes, myriapods, and earthworms, totaling an additional 334 lbs.   Apparently there are no similar determinations of the animal population of our grassland or desert soils.   In all probability the desert microfauna, with the possible exception of the insects, is much smaller than in a more humid area.[2]

Shaler ('92, pp. 285–286) pointed out that the quantity of nutritious bone dust contributed to soils through the death of vertebrate animals, when measured in terms of geologic time, though inconspicuous, is very great.

In many parts of England a weight of more than 10 tons of dry earth per acre annually passes through the bodies of earthworms (Darwin, '90, p. 305).   Quite possibly, in our arid areas, the entire superficial soils layer is worked over in a cycle of years by burrowing rodents, ants, and other animal forms.

Animal droppings may be of measurable influence on soils, especially when sufficient geologic time is allotted for their accumulation and incorporation. Sometimes the influence of excreta is harmful to existing vegetation.   Elton ('30, p. 54) said the manuring action of Arctic Terns in Spitzbergen is rendering the island inhospitable for themselves through its detrimental action on vegetation.   The aggregate of excreta from the normally large numbers of animal organisms must be considerable.   Studies by Murphy ('25, pp. 58–60, 71–73) of the guanay, showed that in 1915 the annual output of its manure shipped from the Peruvian Islands was less than 25,000 tons, while in 1925 it was about 90,000 tons.   Bailey ('28, p. 113) estimates no less than 100,000 tons of the guano of the Mexican freetailed bat removed from Carlsbad Caverns, New Mexico.   These picturesque examples give a hint of the huge figures which would have to be used to express the relations to soils development of the excreta of all living animals in the past and present.

According to Stoklasa ('29) considerable importance in humus building may be attributed to caterpillars, the excreta of which are said to inoculate plant residues with cellulose-decomposing bacteria living in the digestive tracts of the caterpillars.

(2) *Accumulating materials for houses, shelters and nests, and storage of food material.*

The banner-tailed kangaroo rat (*Dipodomys spectabilis* ssp.) of western Texas, New Mexico, Arizona, and old Mexico is an industrious storer of vegetation in its elaborate sub-surface chambers.   During the late winter and spring, and again in the late summer, when vegetation is available, the bannertail stores on an average, for the year, some 4 lbs. of seeds and crowns of grasses and miscellaneous vegetation (Vorhies and Taylor, '22, p. 37).   From

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[2] Breazeale comments as follows: " Personally I have never seen a poor or unproductive soil which contained an abundant fauna.   I am daily getting more and more of the opinion that the results which we get with fertilizers are indirect, that is, we fertilize the soil flora and probably the fauna, and not necessarily the crop.   There is a weak link in every chain and in many an unproductive soil the absence of fauna may be the weak link. Animals certainly bring life and vitamine-like substances into the soil."

a single den in New Mexico were taken 13 lbs. of material. The annual total at the 4 lb. rate for 100,000 banner-tailed kangaroo rats on the Santa Rita Range (50,000 acres) would be 400,000 lbs. or 200 tons per year.

The many thousands of wood rats (*Neotoma albigula albigula*) of the Santa Rita build conspicuous dens of sticks, cactus joints, yucca leaves, and miscellaneous loose material available on the semi-desert. Considerable quantities of food and nest material are transported to and into the den at all times of the year. If the wood rat consumes twice its weight of dry food in a year—a conservative estimate—the amount eaten and metabolized into digestive end products would aggregate more than 80 tons weight on this area alone. These various materials imported or deposited by the wood rat have an appreciable effect on the soils beneath the den. Under each one of the older and larger wood rat houses (belonging to *Neotoma fuscipes annectens*) in the Santa Cruz, California district, Streator ('30, p. 318) notes that one can obtain from 10 to 20 sacks of manure. Hundreds of sacks of this fertilizer have been gathered and shipped to greenhouses, where florists have found it especially beneficial for fern culture. Greene and Reynard ('32) and Greene and Murphy ('32) have reported on soils effects by kangaroo rats and wood rats, though they did not, perhaps, sufficiently emphasize that the effects of animal manuring consist not only in the *addition* of metabolized plant materials, but even more importantly in the *concentration* of nitrogenous matter and its more effective *incorporation* in soils.

(3) *Soils packing.*

The continuous impact of the hoofs of certain large animals such as antelope, moose, elk, caribou, sheep, goat, and deer on soils exercises an important influence, especially in a hilly country and in wet weather. Grinnell ('23, p. 147) has shown that " Close tamping tends to exclude the air and hence to suffocate the plant roots, to which oxygen is as essential as it is to animal life." The geologist Bailey (in Collingwood, '32, p. 419) has pointed out that under the semi-arid conditions of a large portion of the west, the amount of runoff is roughly proportional to the sparsity of plant cover, the loss of surface litter, and the compacting of the soil.

Wherever considerable numbers of large native ungulates persist, their soils tamping is doubtless an appreciable factor. It seems doubtful, however, whether all the wild creatures put together have, or ever have had, as serious an effect in this regard as have domestic livestock, which are often more continuously concentrated on particular areas than their wild prototypes ever were.

(4) *Dam building and flooding.*

Animals may, in a notable manner, change the conditions under which soils develop. The beaver is an outstanding example. Its tree cutting and dam building activities are well and widely known, but some of the far-reaching effects of its engineering operations are not so clearly recognized. The beaver builds a dam and slows the water of a stream. Silt may be deposited and

swamp, marsh, or peat soils develop. So long as the beaver is on the job, however, the water level is maintained. It is only after the animal has moved that the streamway can be altered to something else.

Marsh ('98, pp. 81–82) attributed considerable importance to the beaver as a factor in the development of marsh and forest land. He refers to Milton and Cheadle, London, 1865, as authorities for the statement that nearly every stream between the Pembina and Athabaska rivers, except the large River McLeod, appeared to have been destroyed by the beaver. Like the forest tree that prevents the growth of its own seedlings through affording them too much shade, the beaver tends to destroy the streams important to its existence. Marsh points out, however, that with the reestablishment of forest on the consolidated areas ultimately resulting from beaver flooding, new streams develop, and former conditions are restored.

Kellogg ('34) writing of the biological complex in relation to soils, points out that the destruction of wolves in Itasca Park, Minnesota, has permitted the beaver and deer to increase enormously. The aspens near streams and lakes have been destroyed by the beaver, the young pine reproduction by the deer, resulting in an upset of normal soils development in the area. As Kellogg points out, a delicate balance exists between various parts of the biological complex, the whole being a single evolutionary complex.

In the northern Cascade Mountains in 1920, the writer was impressed with the profound changes in practically all animal and plant life brought about by the beaver. With the inevitable alterations of water and soils conditions, went similar changes in the birds and mammals, as well as, undoubtedly, in the insects, amphibians, and the fauna and flora generally.

(5) *Digging of burrows and associated soils working.*

Twenhofel, in his great Treatise on Sedimentation ('26, p. 78), points out that every animal that digs a burrow in the ground carries the material more often down hill than up. The amount of soils working accomplished by burrowing creatures of different sorts must be very large.

It is interesting to review the extent to which living creatures are intimately connected with soils. Of course, all living things whatsoever, even though not definitely associated with soils, are but one step removed from them. In the case of land plants, a relatively large proportion root directly in soils. Land animals also, are very intimately related to soils, and most spend some part of their life history in them. One needs only to run over the principal phyla—protozoa, sponges, worms, molluscs, myriapods, crustacea, insects, spiders, and chordates, to realize the close connection of most of them with the substratum. McColloch ('26) calls attention to the statement that 95 per cent of all insect species invade soils at some period of their lives. Even the vertebrates, especially the reptiles, amphibians, and mammals, are very closely associated with soils. The reptiles and amphibians hibernate or aestivate in them, some of the birds even, nest in them, and a very large majority of mammals, including most of the rodents and insectivores, and many

of the carnivores and edentates, as well as man, the primate, burrow into them. If one is sufficiently gifted with scientific imagination, he can perhaps picture some of the potentialities of all this animal work on and in the different soils of the world. To obtain a little more adequate concept, one must multiply present work and potentialities by a couple of hundred thousand, the number of years which have gone by since the Pleistocene, not to mention periods previous thereto.

But let us turn to some additional examples of the work of burrowing animals.

Perhaps earthworms have received more than their rightful share of attention. Recorded by Darwin ('90, p. 110) to a depth of 66 inches, other observers have recorded them 7 to 8 feet down. Von Hensen, cited by Darwin, estimated 133,000 living earthworms in a hectare of land, or 53,767 in an acre. Darwin's own estimate of the amount of earth in the castings of these worms was more than 18 tons to the acre under certain conditions ('90, p. 165). Twenhofel ('26, p. 113) writes that lob worms eat the sands through which they burrow, bringing their excreta to the surface like earthworms. Individual lob worm castings have been estimated at 84,423 per acre at any one time or about 50,000,000 per square mile. Following destruction of worms in Lincolnshire, the land is reported (Marsh, '98, p. 129) to have remained sterile until worms reoccupied it.

Garlough and Spencer of the United States Biological Survey found 14,500 crayfish holes to the acre in some fields in Mississippi (unpublished ms.).

Ants and termites have much to do with soils characteristics in certain tropical and arid areas. Brazil is one great ant's nest, says a traveler. Branner ('00, p. 152) suggested that the impression one gets in the tropics is that ants are vastly more important as geologic agents than the earthworms of temperate regions. He observed holes made by ants in Brazil penetrating the ground to a depth of 13 feet. The great numbers of ants is suggested by the fact that there are in Brazil several species of armadillos and ant-eaters which feed in part or entirely on ants and termites (Branner, '96, p. 300). Termite nests of clay range from 1 to 12 feet in height and 1 to 10 feet in diameter. In places one could almost walk on termite nests for several hundred yards at a time, says this author.

Nefedov ('30) reported on a quantitative study of the ant population of the Troitsk Forest Steppe Reserve (Russia). Ant nests, it seems, are very numerous in steppe regions. In the chernozem soils 415,000 nests per square km. were found; in alkali soil, 340,000; in saline regions 257,000. Some species were present in all soils, differing in numbers, however, on different soils. Others were found mainly on certain soils, absent on others.

Wheeler ('30, p. 66) quotes Lameere to the effect that the ant, *Messor arenarius,* is the most powerful organism of the Algerian desert. This species makes clusters of craters each 50 cm. in diameter, the galleries probably

extending down into the soil for several meters. Reports indicate nests of single colonies covering more than an acre of sand.

Observations in Kansas by Bryson ('31, p. 22) indicated that all burrowing insects that go below 6 inches will effect a gradual interchange of soil and subsoil in varying amounts. He concluded (p. 24) that insects play no small part in intermixing the soil when the various layers are fixed in their positions.

On the Santa Rita Experimental Range near Tucson, Arizona, Reynard and Thrift (unpublished ms.) found an average of 13.1 cubic feet of soil actually displaced by the burrowing of the banner-tailed kangaroo rat. If there are 100,000 dens on the Range, as indicated by some counts by the writer, the total weight of earth displaced would aggregate 48,518 cubic yards, or approximately 3,639 tons. Seton in 1882 first pointed out the soils work of pocket gophers in western Canada (Seton, '09, pp. 578–586). A recent estimate is that in five months these animals do as much work in soils mixing as earthworms do in five years. Making application of the same theme in California, Grinnell and Storer ('23, pp. 143–144) estimated that pocket gophers in Yosemite National Park in the course of a year handled 160 carloads of earth of 50 tons each or 8,000 tons, altogether. It is pointed out that the pocket gopher of Rancho la Brea (Pleistocene) is identical with that of the present day. If the pocket gopher has been active for so short a period geologically as 200,000 years, the soils turn-over, at the rate of $\frac{1}{10}$ inch per year, would total 1,700 feet, or the equivalent of 3,400 plowings to a depth of 6 inches. These authors give an excellent summary ('23, p. 141) of the relation of the pocket gopher to its environment.

Given the combination of large numbers of animals and long periods of time a lot can be accomplished. Kashkarov and Kurbatov ('30, pp. 48–49) found a dense population of the large gerbille (*Rhombomys opimus*) on the Kara-Kum Desert in western Turkestan, their counts indicating 187 burrows per acre. Grinnell and Jacobsen (see Grinnell and Dixon, '19, p. 654) note that the Oregon ground squirrel occurred in Butte County, California, at the rate of 560 open burrows to the acre.

Organisms which are very numerous, though small, probably exercise a greater effect on soils than larger forms which are less abundant. Also, as Branner pointed out ('96, p. 295) referring to ants and termites, the number of species, in a problem of this sort, is a matter of little or no importance as compared with the number of individuals and their habits. The same author writes that the chemical agencies important in the decomposition of Brazilian rocks consist of two types, organic and inorganic; that of these the organic acids are the more important; and that these acids are derived from two sources, burrowing animals and plants. Here is a significant hint as to one of the ways in which organic reactions work.

(6) *Promoting erosion.*

Jones (Watershed Handbook, U. S. Forest Service, '23, mim., p. 6) asserts that in general overgrazing is responsible for much more abnormal erosion than all other causes combined. It is obvious that rodents and cer-

tain ungulates, often themselves heavy eaters of soil-binding vegetation, may become auxiliaries in the pervasive and destructive accelerated erosion which is so widespread throughout the range country.

The same burrowing rodents may be beneficial in some places and detrimental in others. Nelson ('30, p. 147) pointed out that the work of pocket gophers in soils is often of the most beneficial character, although on bare slopes their work is injurious in that it increases erosion of the fertile surface strata.

Branner ('96, p. 297) quotes Wood who reported sauba ants in South America having ruined a gold mine for a time, by breaking into it with a tunnel some 80 yards in length and letting in a torrent of water, which broke down the machinery and washed away all the supports.

Munns ('29, pp. 5–6) opines that the buffalo, operating much the same as large herds of cattle in the early days, was the direct cause of much erosion and soils loss. There was a difference, however, in that the grazing was diffused rather than continuously concentrated. As a result, it was probably much less destructive than the work of livestock in some places in modern times.

There seems to be little or no evidence of a critical character that rodents or other animals, under natural conditions, promote soil erosion.

(7) *Preventing erosion.*

In proportion as animals increase the absorption of water by soils, promote favorable soils conditions for the establishment of a vegetation cover, and assist in the process of scattering and planting of vegetation, they tend to prevent erosion. Under natural conditions animals were a part of what Lowdermilk ('34, p. 532) calls the geologic norm of erosion. The cause of the accelerated erosion which has become so great a national problem is the destruction of the native mantle of vegetation, as Lowdermilk points out, through fire, destructive lumbering, heavy grazing, smelter fumes, railroad and highway cuts, clearing and cultivation for agricultural crops. The activities and reactions of organic life, including animals, on soils are undoubtedly for the most part beneficial. As Marsh ('98, p. 55) says ". . . every plant, every animal, is a geographical agency, man generally a destructive [element] ; vegetables, and in some cases even wild beasts, restorative powers."

(8) *Soils are complicated structures.*

One may perhaps fairly regard a natural soil as comparable with a complicated building. It possesses definite structure. It is inhabited by a significant community of plants and animals, which, under natural conditions, work together to form a rather harmonious and productive whole. But many things can happen! Disturbance of the structure of the soil, removal, in any manner, of a part of its organic inhabitants or the addition of others, alteration in the water content and the chemicals associated with such processes as irrigation, evaporation, drainage, or fertilization, are certain to modify the soil. Under suitable conditions the soil becomes even more productive than

it was originally, temporarily at least; under others it is depleted through actual removal of material or some other form of impoverishment.

Romell ('30, p. 842) says: " Burger, with good reason, compares the agricultural soil to an unorganized mass of building material, whereas the natural forest soil, with its definite, stable organization, is like a house built from this same material." And further (p. 843) : " It is more and more generally recognized that a natural soil, like a living organism, must be studied as a whole to get a correct idea of its responses."

## SUMMARY

1. The environment not only acts upon plants and animals, but these living things react on their environment, particularly on soils. The reactions of vegetation on the substratum are well known. Less study has been given to animal influences, although at present they are receiving increased attention.

2. The accumulation in soils of excreta, hairs, horns, skins, feathers, scales, and other shed parts of animal bodies, and in the end, the bodies themselves, must have a good deal of influence on the structure and composition of various soils. The weight of the animal population, even on (and in) grassland or desert soils, undoubtedly totals up to an appreciable poundage. When it is realized that the processes of natural soils working, and of accumulation of organic matter have gone on for a good many hundred thousand years, one may form a more adequate idea, perhaps, of potential animal soils effects (Darwin, '90, pp. 305–313).

3. Besides the excreta and bodies, there is the accumulation on or in soils of materials for the houses, shelters, and nests of animals, and for their food.

4. The pounding of the surface by heavy-footed quadrupeds during wet weather or in hilly country tends to consolidate certain soils, thus excluding the air and tending to suffocate plant roots.

5. Stockmen and scientists alike are recognizing increasingly that overgrazing by livestock, supplemented by the work of rodents, insects, and other forms, is one of the most important conditions responsible for the widespread accelerated soils erosion so common on range lands. Channeling or tunnelling by burrowing animals is sometimes serious.

6. Dam construction by the beaver is well known. The extent to which the beaver is associated with the development of soils over the North American continent is less appreciated. In bringing about alterations of its environment from stream to pond, then to meadow, and finally to climax forest, the beaver is responsible for profound changes, not only in the substratum, but in the entire fauna and flora. The beaver is the great original check-dam engineer. Its work in water conservation and prevention of erosion is widespread and important.

7. In improving the water-holding capacity of soils through natural cultivation and in disseminating and inadvertently planting soil-binding vegetation, animals in general help to prevent erosion. The work of animals tends also to promote aeration of soils and the formation of humus.

8. Digging of burrows and soils working are characteristic animal activities, found in some groups of most of the phyla of animals, and particularly important in the worms, insects, and vertebrates. It seems probable that in places the ant, and in others the pocket gopher (Grinnell, '23, pp. 144–145) far surpass the earthworm in extent of soils working.

9. By bringing earth to the surface where it can wash or blow away, animals promote normal down-hill movement of loose material, thereby tending to level off surface inequalities.

10. Soils working by animals tends to undermine stones or other hard objects, finally bringing about their disappearance beneath the surface.

11. The work of animals contributes to the deepening of soils (Grinnell, '33, p. 295) through their burrow systems which carry air and water with contained substances to lower levels.

12. Animal effects on soils embrace not only addition of disintegrated and decomposed plant and animal remains, but even more importantly, probably, the concentration of nitrogenous matter and its more effective incorporation in soils. Occasionally the concentration of nitrogenous material is excessive; but usually it appears to be beneficial to plant life. Animals are responsible, in part, for the organic acids which are important factors in soils making.

13. While soils disturbance of various sorts may promote a great increase in production, as in plowing, cultivation, fertilization and associated farm practices, in some instances conditions are encountered which are detrimental to production (*e.g.* accelerated erosion, " freezing " of surface soil layers so they will not take water, water-logging, desiccation). Disturbance affects not only the soil structure and soil plants, but also the animals of the soil. Animal factors exercise an appreciable influence on soils in certain instances, and should always receive attention.

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# THE ROLE OF WESTERN WHITE PINE IN FOREST SUCCESSION IN NORTHERN IDAHO

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## INTRODUCTION

The importance of vegetational studies in virgin forests has become more and more obvious during the past few years as a result of the increasing scarcity of primeval areas. The work of Cooper ('13) on Isle Royale, Michigan; of Nichols ('13) at Colebrook, Connecticut; of Lutz ('30) at Heart's Content, Pennsylvania; of Gates and Nichols ('30) studying an area near Pellston, Michigan; and of Hough ('32) in Pennsylvania, may be said to compose the greatest portion of the meagre literature on this subject.

With a view, therefore, to obtaining knowledge of the character of the vegetation of the sub-climax and near-climax forest of the " western white pine type," these studies were undertaken, in three virgin communities. Although there have been several general surveys and observational studies made on this subject in the Northern Rocky Mountain region, there is no published work available on the vegetation of specific areas. It is the purpose of this paper, therefore, to present such data.

In his more or less extensive observations in the Bitterroot Mountains of northern Idaho, Larsen ('29) notes that after fires, the succession is somewhat as follows: The intolerant and drought-resistant western larch and lodgepole pine represent the first stage. These trees, with an initial stage of subordinate vegetation, prepare the site for the advent of Douglas fir and western white pine, and a second layer of lesser vegetation. This stage in turn paves the way for the climax forest association of western red cedar, western hemlock, and lowland white fir with a typical sparse shrubby and herbaceous vegetation (fig. 1).

Accepting these general relationships, the areas investigated in this study may be placed in the second stage in the case of areas 1 and 2, while area 3 probably belongs to the climax or near-climax stage.

In a general way the three areas belong to the white pine type, so termed because of the volume and economic value of *Pinus monticola,* rather than because of the number of trees per acre or its importance in the climax forest. Briefly, this type consists most commonly of western white pine, *Pinus monticola,* as the dominant species with other trees subordinate. With age,

FIG. 1.  Near-climax forest, showing absence of white pine; general lack of shrubby and herbaceous vegetation, and abundance of cedar and hemlock reproduction.  Veteran larch at the right.—Photo by K. D. Swan.  Courtesy of U. S. Forest Service.

however, the stand changes and consists chiefly of western red cedar, *Thuja plicata;* western hemlock, *Tsuga heterophylla;* and lowland white fir, *Abies grandis;* with occasional veterans of Douglas fir, *Pseudotsuga taxifolia,* and western larch, *Larix occidentalis.* The subordinate vegetation is very sparse, but quite uniform on the three areas.

To study the composition of this association, therefore, strips were laid out through each of the areas for a tally of the overwood, and quadrats laid along these strips to study the shrubby and herbaceous vegetation, and reproduction of the tree species. Site conditions were also studied.

## THE AREA

The Priest River Branch of the Northern Rocky Mountain Forest and Range Experiment Station occupies about seven square miles of the Kaniksu National Forest in T. 58 N., R. 3 and 4 W., in Bonner County, Idaho, fifteen miles northeast of the town of Priest River.

This area is made up of three topographic types: " the first, rugged mountainous provinces, composed of tilted, faulted, metamorphosed sediment, massive basic igneous sills, and a batholithic acid igneous intrusion with its attending stocks and cupolas; second, plateau-like areas, lower than the mountain masses, planed off by continental-glacier erosion; and third, stream-valley plains." [2]

The Experimental Forest is drained by the East River, Benton Creek, and Fox Creek, all of which flow west into the Priest River, a glaciated, fault-formed valley.

Areas 1 and 3 are on stream-valley plains. Area 2 is in the rugged-mountain province.

Elevations range from below 2240 feet on the river flats to 5700 feet at the Experimental Lookout Station, giving a relief of almost 3500 feet.

## GEOLOGY AND SOILS

Igneous and metamorphic rocks of the Pre-cambrian, sedimentary materials of the Pleistocene, and Cretaceous intrusions are all represented here.

The underlying rocks in the Experimental Forest consist chiefly of granites overlaid by schist and quartzite, very near the surface in some places and outcropping in others.

Horizontal (profile) development resulting from weathering is notably absent in the majority of the soils, except in a few instances. The subsoils are generally friable and free from marked compaction.

The organic debris on area 1 consists of an *F* horizon (Hesselman, '26) of 1–2 inches made up of 2 or 3 years' fall of needles, light brown in color, merging into a half-inch partially decomposed *H* horizon, dark brown in color, which is only very slightly if at all mixed with the mineral soil. Below this,

[2] **Kirkham, V. R. D., and E. W. Ellis.** 1926. Ore Deposits of Boundary County, Idaho. *Bur. Mines and Geol. Univ. Idaho Bull. 10,* p. 10.

to 40 inches, is a gray-to-brown sand with coarse gravel. All layers are distinctly micaceous. This is called the Springdale sandy loam by Lapham and Young ('25), who are not certain as to whether the material is glacial outwash or alluvial in origin. The substratum (which was not reached in the present examination) to a considerable depth consists of old lake clays, and occurs on old stream terraces lying above the level of the present water courses. The surface drainage is good and the subdrainage is generally excessive. The water holding capacity is low, thus minimizing the upward movement of the capillary moisture.

Area 2 lies on the Huckleberry fine sandy loam. Below the organic debris made up of a 2-inch $F$ layer of light brown needles, chiefly pine and hemlock, and a dark brown half-inch $H$ layer, is a 12-inch stratum of·yellow brown fine sandy loam, with small amounts of angular stones. For 6 inches below this there is a gray-brown sand with more angular rock material. Below this is found broken, decomposed schist and quartzite which merges into the bedrock. As is to be expected, soils of steeper slopes, as here, are shallower than the average of the same soil type. The steepness of the slopes results in excessive surface drainage. The water holding capacity of the soil is good except in shallow spots. The south slopes tend to dry out quickly.

On area 3 the Mission fine silt loam is the prevailing soil type. The organic debris consists of a dense $F$ layer of 1.5 inches of light brown to darker material, without any well defined $H$ layer. Below this, to a depth of 18 inches, is a yellow-brown very fine silt loam, containing much mica. Below 18 inches is a compact, rusty-spotted gray clay, which appears to be an old-lake deposit resulting from the extension of the arms of the lake up the various creeks which now drain the forest. The deposit is many feet in thickness. The soil has a smooth to slightly rolling surface, good drainage generally, and good moisture-holding capacity. A mechanical analysis showed 50–55 per cent silt, 30–35 per cent sand, and 10–15 per cent clay.

For the most part, the soils of these three plots are acid in reaction with a pH ranging from 6.2 to 6.5.

## CLIMATE

Weather records have been kept for 22 years at the Priest River Experiment Station on the Experimental Forest. A 20-year summary (Jemison, '32) makes available the following data.

The mean annual precipitation is 28.29 inches, and its distribution by months is shown in table I. The average annual snowfall is 81.8 inches. The greatest snow depth on the ground was 46.2 inches in the winter of 1931–32; the least was 7 inches in 1920–21. The prevailing wind direction is SW, all the year around. The wind velocity at the 150-foot level has a highest average of 20 miles per hour, with a highest recorded maximum of 38 miles per hour (based on sudden gusts of a few minutes' duration). The average wind velocity at the 8-foot level is 1.6 miles per hour. Monthly

maximum, mean, and minimum temperatures are shown in table I. The length of the frost-free season is about 62 days. The average date of the last freezing temperature in the spring is about June 20; the earliest in the fall is about August 20. The tree-growing season is 203 days, based on the number of days when mean air temperature is above 40° (Livingston and Shreve, '21).

TABLE I. *Mean Monthly Temperatures and Precipitation at Priest River, Idaho* °

| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Degrees Fahrenheit | | | | | | | |
| Maximum | 30.0 | 36.9 | 45.9 | 57.3 | 66.1 | 74.0 | 83.4 | 82.1 | 69.7 | 56.0 | 39.6 | 31.3 |
| Mean | 23.0 | 27.5 | 34.7 | 43.1 | 50.7 | 57.6 | 63.8 | 62.4 | 53.1 | 43.3 | 32.7 | 25.1 |
| Minimum | 16.1 | 18.2 | 23.5 | 29.0 | 35.3 | 41.3 | 44.3 | 42.7 | 36.6 | 30.6 | 25.9 | 18.9 |
| | | | | | Inches | | | | | | | |
| Precipitation | 3.60 | 2.87 | 2.41 | 1.93 | 2.01 | 1.78 | 0.86 | 1.21 | 1.84 | 2.41 | 3.59 | 3.78 |

° Based on 20 year records of the U. S. Forest Service.

## HISTORY

First settled in 1842, Idaho was admitted into the Union in 1890. In 1897 the land drained by the waters of the Priest River, Priest Lake, and Upper Priest River—an area approximating some 645,000 acres—was set aside from the public domain by proclamation of President Cleveland, to be known as the Priest River Forest Preserve. Ten years later President Roosevelt withdrew an additional area to the west, and in 1908 the whole became the Kaniksu National Forest. About 4,500 acres on the Kaniksu were set aside in 1909 to form the Priest River Experiment Station.

Area 1, known as the Knoll Plot, was left for seeding purposes on one of the earliest forest service timber sales; area 2 was set aside as a Natural Area; and area 3 was left for lack of a suitable market due to declining prices, absence of fires, and finally for experimental purposes.

## VEGETATION

### Methods

Due to the small size of areas 1 (3 acres) and 3 (2 acres), it was impossible to gridiron the stands completely, but a strip 1 chain wide was run through the stand, and plots were established at half-chain intervals. Although area 2 (150 acres) was sufficiently large to permit gridironing, a Management Plot established by the Experiment Station in 1927, as typical of this stand, was divided into smaller plots for the purpose of this study.

In laying out the plots, a standard forest service compass and steel tape were used. The lines were run from edge-of-timber to edge-of-timber, beginning and ending far enough in from the edge to avoid the influence of the

surrounding or adjacent cut stands. Tree diameters on the plots were measured with a steel diameter tape.

All trees above 1 inch at breast height (4.5 feet above the ground) were measured. All below 1 inch D.B.H. were counted on the entire plot. Ten milacre quadrats were established on each area, marked by cedar stakes (as was the center line through the plots, at half-chain intervals). The identification of the plants was checked against the herbarium specimens of the Experiment Station.

The tree nomenclature is that of Sudworth ('27) ; nomenclature of shrubs and herbs is that of Piper and Beattie ('14).

Phytographs (Lutz, '30), as shown in figure 4 are used to show the ecological position of the various species of the association. The criteria used to determine the relative importance of the species are: Abundance percentage, frequency percentage, number of size-classes present, and basal area in square feet per acre. In a standard chart, constructed to aid in the comparison, the following values are assumed: Abundance 100 per cent, frequency 100 per cent, four size-classes present,[4] and a basal area value of 300 square feet per acre.[5]

## Communities

Apparently because of the high market value and wide occurrence of white pine in the region, foresters have applied the name white pine type to this association which ought, more appropriately, to be called the cedar-hemlock-white fir association. Larsen ('30) classified this type as the " Mesophytic transition forest," and as the cedar-hemlock-white fir type. Occasionally there occur in this region small areas of a white pine consociation, but for the most part this species plays a minor part in the climax forest. It is, however, important, because in the presence of a seed source, openings due to windfall or other agencies are readily taken over by white pine.

### AREA 1. GENERAL CHARACTER

Despite the heavy density of this high coniferous forest with an almost complete canopy, some light does penetrate to the forest floor. On the average, however, this light does not amount to more than 3-5 per cent of full sunlight. The diameters of the larger white pines are noteworthy; occasional trees attain diameters of 37 or 38 inches. Rarely a cedar reaches 40 inches. The presence of 364 stems per acre is less than on the other two areas. There is little difference, impossible to measure by methods now available, in the density of the three areas. Windfalls are very common on this as well as on the other two areas, but no data on age or species of down trees were ob-

[4] The size classes used are: 1. Small reproduction; up to 0.9 in. D.B.H. 2. Large reproduction; 1.0–3.5 in. D.B.H. 3. Small trees; 3.6–11.5 in. D.B.H. 4. Large trees; 11.6 in. D.B.H. and up.

[5] This value of 300 square feet is used because it represents approximately the average maximum per acre in this vicinity.

tained.  The forest floor has a very sparse covering of shrubby and herbaceous vegetation.  This, in conjunction with the general lack of reproduction, gives a single-storied aspect to the forest (fig. 2).



Fig. 2.  Typical view through area 1, showing predominance of white pine.  Note lack of herbaceous and shrubby vegetation and abundance of down timber.

Abundance and frequency are given in table II for all tree species, as well as for subordinate vegetation.  The fact that there are only 6 species of trees, and only 12 of herbs and shrubs, may be interpreted to indicate the advanced ecological character of the community.  None of the arboreal, herbaceous, or shrubby species show any exclusiveness in this community, but differ only in frequency and abundance between areas.

In abundance the ranking is hemlock, white fir, cedar, and white pine.  In frequency, hemlock and pine rank first, with cedar and white fir second.  The most common shrubby and herbaceous vegetation consists of *Coptis occiden-. talis, Berberis repens, Vaccinium macrophyllum,* and *Linnaea borealis longiflora,* from the standpoint of both frequency and abundance.

TABLE II. Abundance and Frequency of Species Found at Priest River, Idaho

| *Trees | Area 1 | | Area 2 | | Area 3 | |
| --- | --- | --- | --- | --- | --- | --- |
| Scientific Name | Abundance percentage | Frequency percentage | Abundance percentage | Frequency percentage | Abundance percentage | Frequency percentage |
| Tsuga heterophylla | 43.9 | 100 | 58.4 | 100 | 67.2 | 100 |
| Pinus monticola | 15.4 | 100 | 3.2 | 40 | 1.5 | 10 |
| Thuja plicata | 16.4 | 90 | 32.3 | 100 | 24.2 | 100 |
| Abies grandis | 20.9 | 90 | 3.5 | 50 | 4.4 | 70 |
| Larix occidentalis | 1.7 | 30 | 0.4 | 10 | 2.7 | 70 |
| Pseudotsuga taxifolia | 1.7 | 30 | | | | |
| Abies lasiocarpa | | | 2.2 | 40 | | |
| †Shrubby and Herbaceous Vegetation | | | | | | |
| Acer glabrum | 1.2 | 20 | 7.0 | 20 | | |
| Actaea rubra | 0.3 | 10 | 0.5 | 10 | | |
| Amelanchier alnifolia | | | | | | |
| Arnica cordifolia | .3.7 | 60 | 8.5 | 50 | | |
| Berberis repens | | | | | 1.0 | 10 |
| Chimaphila umbellata | 1.4 | 30 | 0.5 | 10 | | |
| Clintonia uniflora | 72.0 | 90 | 29.5 | 100 | | |
| Coptis occidentalis | | | | | 78.5 | 100 |
| Disporum trachycarpum | | | 1.0 | 10 | | |
| Linnaea borealis | 2.3 | 50 | 10.5 | 70 | 5.0 | 40 |
| Lonicera utahensis | 0.2 | 10 | 7.5 | 40 | | |
| Menziesia ferruginia | | | 3.0 | 10 | | |
| Pachistima myrsinites | | | 5.0 | 60 | | |
| Pyrola bracteata | | | 2.0 | 30 | | |
| Rosa sp. | 0.7 | 20 | 2.0 | 10 | 4.0 | 30 |
| Sorbus sambucifolia | | | | | | |
| Taxus brevifolia | 0.8 | 10 | 3.0 | 40 | | |
| Tiarella unifoliata | | | | | 2.5 | 10 |
| Trillium ovatum | | | 2.0 | 20 | | |
| Vaccinium macrophyllum | 3.5 | 50 | 21.0 | 70 | 7.0 | 30 |
| Vagnera sessilifolia, | 1.5 | 20 | 1.0 | 10 | 2.0 | 20 |
| Viola sp. | 1.4 | 30 | 5.5 | 60 | | |

* Based on a total of 10-.05 acre plots on each area.
† Based on a total of 10 milacre quadrats on each area.

## Human Influence and Fire

There has been no cutting on the actual area studied, but on all sides of the area it has been quite extensive. The difference in conditions between the cut-over and the virgin stands is very marked.

Although there is no evidence of recent fires on this area (a very fortunate and unusual fact in a region of such high fire hazard), there is ample evidence of early fires on the area as a whole. The even-aged character of the white pine points strongly toward early fires on the Kaniksu and elsewhere in northern Idaho. Marshall ('29) found, by examinations of annual rings, evidences of fires on nearby white pine stands in 1610, 1641, 1687, 1742, and 1843.
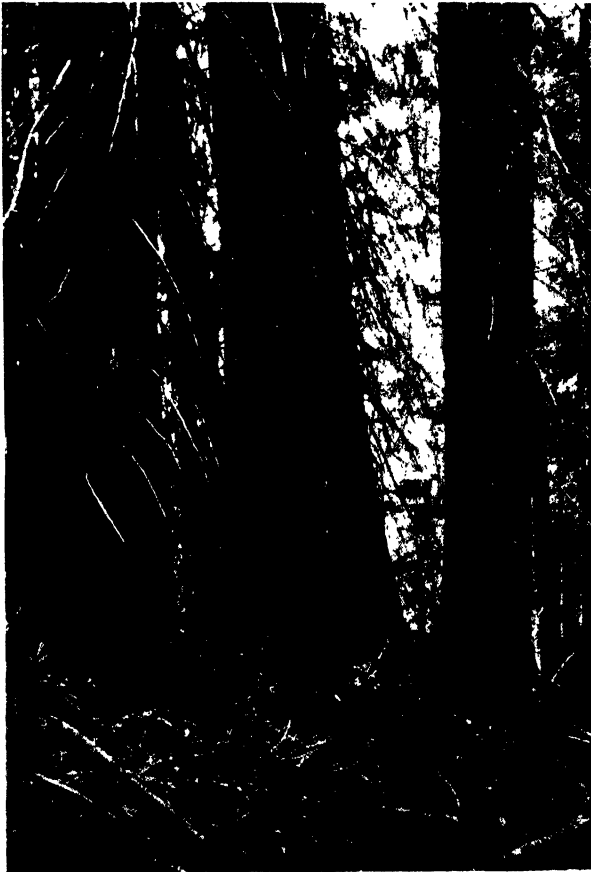


FIG. 3. Forest stand on area 2, with an occasional white pine among the cedar and hemlock. Herbaceous vegetation is sparse.

Lieutenant R. Saxton, U. S. A. ('53), noted in his diary on August 13, at which time he was at the outlet of Lake Pend Oreille: "We were . . .

discouraged by accounts of the route from this place to St. Mary's village given by a Scotchman who has recently passed over it. He says that for five days' journey there is no grass, it having been burned over by the Indians." (There is a possibility that ' St. Mary's village ' referred to Hamilton, Montana.)

"August 16. The woods are on fire in many places—evidently for the purpose of retarding our progress."

"August 18. The route has been through dense forest, either burning or just burned, the ground being very hot for the animals' feet."

There is ample evidence that fires have occurred and reoccurred in many parts of this region. These are important from the standpoint of white pine invasion. Lutz ('30) found similar results with *Pinus strobus* in Pennsylvania.

## AREA 2. GENERAL CHARACTER

In general this area is similar to area 1, differing somewhat in being steeper in slope, at 1000 feet higher elevation. White pine is less prevalent than on area 1 (fig. 3).

As in the case of area 1, the stand is of a one-storied character, although a more or less definite understory of cedar and hemlock is evident. The vegetation consists of 6 arboreal and 17 herbaceous and shrubby species. Of this vegetation no species shows any exclusiveness; they differ only in frequency and abundance, the trees ranking as follows: hemlock, cedar, white fir, white pine, alpine fir, and western larch. The herbaceous and shrubby plants in order of importance are: *Clintonia uniflora, Vaccinium macrophyllum, Linnaea borealis longiflora, Viola* sp., *Pachistima myrsinites,* and *Arnica cordifolia.*

### Human Influence and Fire

There has been no cutting on this area, and no evidence of recent fire could be found on the area itself.

The point to be noted here is that the hemlock and cedar both increase in importance, but the white pine is less important than on area 1 (fig. 4).

## AREA 3. GENERAL CHARACTER

The only general difference between this area and the others is the extreme sparseness of the lesser vegetation, and the almost complete absence of white pine, except on one edge of the stand where a small brush-disposal fire from an adjacent cutting temporarily escaped control and made a slight opening.

The windfall on this area is somewhat heavier, and just two years ago the last white pine snag fell, after having stood in a dead condition for many years. The absolute lack of white pine except at the borders of the stand and where the small fire occurred is noteworthy (fig. 1).
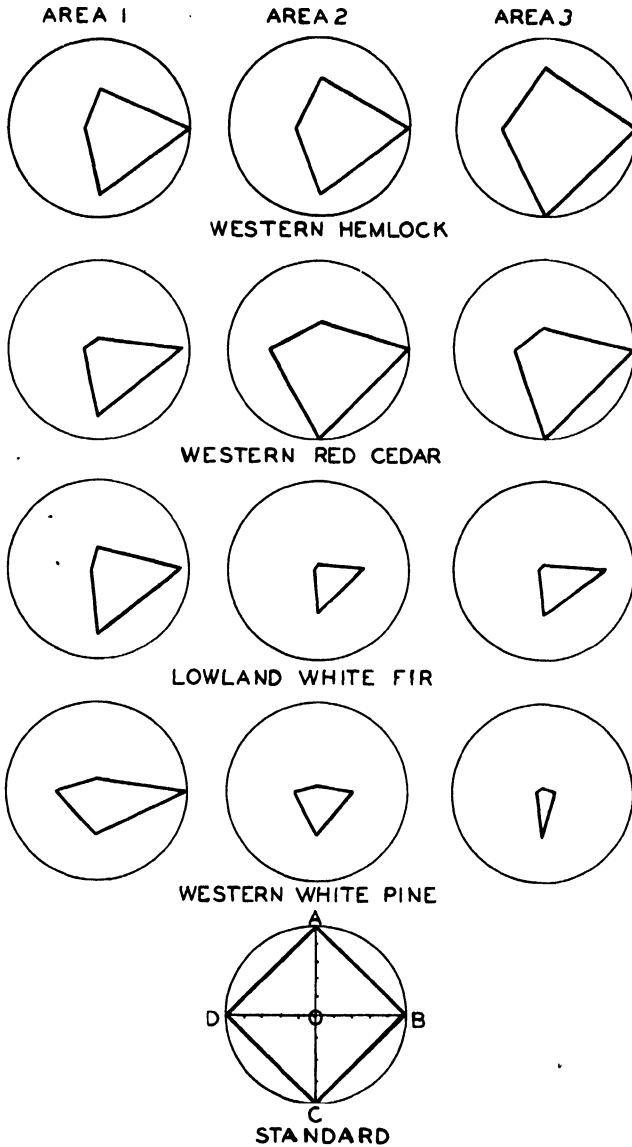
FIG. 4. Phytographs for the principal tree species on the three areas. Legend for standard: $AO$ = Abundance percentage, each division of the scale indicating 20 per cent; $BO$ = Frequency percentage, each division of the scale indicating 20 per cent; $CO$ = Number of size-classes present, each division of the scale indicating one size-class; $DO$ = Basal area in square feet, each division of the scale indicating 60 sq. ft.

The one-storied character is practically absent here due to the many-aged character of the stand. The number of herbaceous and shrubby species is 7, while there are only 5 trees. On the basis of frequency and abundance the ranking is: hemlock, cedar, white fir, western larch, and finally white pine. In the case of the subordinate vegetation the ranking is: *Coptis occidentalis, Linnaea borealis longiflora, Vagnera sessilifolia, Rosa* sp., and *Viola* sp.

### *Human Influence and Fire*

There has been no cutting on the area itself, but some of the timber immediately surrounding the area has been felled. This, and the presence of a county road along one side of the stand, alters the light, moisture, and temperature relationships along the border. Where the small brush fire escaped temporarily on one side of the stand, a few white pines have been able to gain a foothold.

The phytographs show how the hemlock, cedar, and white fir increase in importance, while the white pine is reduced almost to naught (fig. 4).

### SUCCESSIONAL RELATIONS

Cooper ('13) in his studies on Isle Royale used as proof of the climax condition of the forest: mesophytism, uniformity of development, formation of such a forest from all successions, and maintenance of equilibrium within the forest.

In attempting to apply these criteria to area 3, the cedar-hemlock-lowland white fir association, we find that although the present studies supply no actual data on this point, general observations elsewhere in the region show that this association tends to be more mesophytic, or less xerophytic, than earlier successional stages. Larsen ('30) classified this association as a mesophytic transition forest; and he ('29) also pointed out that the cedar and hemlock required moister conditions than associated sub-climax species. As to uniformity of development, the few places where this association can yet be observed show the presence of the same tree species and lesser vegetation, bearing the same relationship to each other. Although the scope of this study is too limited to permit of the conclusion that all successions lead to this association, we can say that examples of the " western white pine type " observed almost always lead to such an association. This is confirmed by Larsen ('29) and by Miller, *et al.* ('27) in their studies in other parts of this region. That the stand is in equilibrium is shown by the prevalence of reproduction of the climax species on area 3, and by the lack of reproduction of sub-climax species. Studies of the individual species making up the association, by Miller, *et al.* ('27), confirm this. The present study shows that only as a result of certain disturbing influences are sub-climax species able to gain a foothold.

Whereas this case is not absolutely proved, there is definite evidence that the western red cedar-western hemlock-lowland white fir association is the climax forest.

To examine the steps leading to this climax is the next objective. The phytographs, as mentioned above, give a more or less complete picture of the successional relationships of the three areas (fig. 4). Age counts and ranking in abundance by size classes are significant in this respect.

This latter point is, perhaps, of greater significance. It is axiomatic, of course, that to appear in the climax forest a species must be able to reproduce and become established under itself and associated species. Unless a species can do this, it can appear only in the earlier stages of the succession. From this point of view, hemlock, cedar, and white fir may be expected to form the climax stand; and for this reason, white pine must appear only in the earlier stages, except where openings occur in the climax stand. For the same reason western larch and Douglas fir are unable to play an active part in the climax.

The evidence presented in the tables appears to point to the following succession: After some major disturbance, usually fire, and depending on the severity of the catastrophe, the comparatively drought resistant western larch and Douglas fir are the first tree invaders. White pine germination is usually abundant on burned seedbed conditions, so that this species is often a first invader. Western red cedar and western hemlock may appear at this point if the site has not been affected too severely or the burned area is not too large in extent. Generally, however, the first association is white pine, Douglas fir, and western larch.

As a result of abundant seed crop and the effect of these trees and subordinate vegetation on the soil, the pine and Douglas fir tend to become dominant. As these species approach maturity and form a complete canopy, the tolerant hemlock, cedar, and white fir are able to become well established. As the site factors are changed, therefore, by the temporarily dominant larch, and intolerant Douglas fir and white pine, these latter species are unable to become established under their own canopy. The overmature veterans become decadent and weak, too weak to withstand windthrow, insects, and decay, and soon begin to drop out. On the other hand, the hemlock, cedar, and white fir thrive, reach maturity, reproduce, and become established and stabilized as the climax association. As stated earlier, the white pine undoubtedly will remain a factor, though an unimportant one, in the climax, coming into openings resulting from windfall or other causes, if seed is available.

To attempt to set down the exact number of years required for each step of the succession is practically impossible. The length of the successional periods will vary with the site conditions involved. A rough approximation of the length of time required before climax conditions are reached, under Priest River conditions, would be about 300–350 years; white pine would reach its peak at 120–180 years, dropping out over an interval of 40–80 years or more; and stabilization of the climax species in 40–60 years after this. It must be borne in mind that this is only a rough approximation, based on what is too meagre data.

It would be of interest to confirm this by examinations of as many un-touched " white pine " stands as possible (and there are not many left in this region) before they are all cut or burned.

Of interest is the increase in basal area, and consequently in volume, as the succession progresses to the climax.   Area 3 has the highest basal area. Lutz ('28, '30) found similar results in New England and Pennsylvania. This greater basal area may be attributed to a more complete utilization of the soil and the air in the climax forest than is true in the earlier successional stages.

## SUMMARY AND CONCLUSIONS

On three virgin areas of so-called " white pine type " in northern Idaho at the Priest River Experiment Station, plots and quadrats were established to study the arboreal, herbaceous, and shrubby vegetation.   Soil wells were dug, and increment borings taken on all three areas.   The first two areas were found to be in sub-climax stages, the third very near to climax.

From the data of size-class distribution, basal area, abundance and fre-quency percentage, were constructed phytographs for purposes of compari-son.   The evidence presented clearly shows that white pine plays a very minor part in the climax forest.   For the most part it appears in the early stages of succession, giving way to the climax association of western red ·cedar, western hemlock, and lowland white fir, shortly after passing maturity.

The climax stand is characterized by a marked sparseness of shrubby and herbaceous vegetation.   The most common species present are *Arnica cordi-folia, Berberis repens, Clintonia uniflora, Coptis occidentalis, Linnaea borealis longiflora, Pachistima myrsinites, Rosa* sp., *Vaccinium macrophyllum, Vag-nera sessilifolia,* and *Viola* sp.

At the present time the high susceptibility of white pine to the white pine blister rust, *Cronartium ribicola* Fischer, and to the mountain pine beetle, *Dendroctonous monticolae* Hopk., might also be considered as a temporary factor in accelerating the successional development towards the climax.

As a result of these successional relationships of western white pine, it can readily be seen that there is a problem in developing a method of manag-ing this type in such a way as to prevent the replacement of the highly valu-able white pine by the less valuable climax species.   The solution undoubtedly lies in an early cutting age, as now recommended and practiced by the Forest Service.

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# STUDIES IN NOCTURNAL ECOLOGY, III. RECORDING APPARATUS AND FURTHER ANALYSIS OF ACTIVITY RHYTHM

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## RECORDING OF ACTIVITY

The first measurement of nocturnal activity by recording apparatus was by Johnson ('26). Relatively heavy animals were used, *e.g.*, forest deer mice, which allowed a simple technique to be employed. This consisted in placing a mouse in a light-weight cage suspended by rubber bands. An indicator fastened to the cage traced the animal's movements on a record made by a paper disk turned by clock mechanism. Unfortunately the apparatus, though simple, was neither figured nor fully explained; neither was the temperature, which varied seven degrees, nor presumably the humidity, adequately controlled. The work was important, however, in that it recorded nocturnal activity, and gave an insight into the behavior of characteristic forest rodents.

Quite recently Davis ('32, '33) has reported an improved apparatus of the same general type for recording the activity of small mammals.

Turning from mammals to the insects, the only other group of animals in which nocturnal activity has been measured by recording apparatus, significant work has been done by Lutz ('32a, b) on three species of Orthoptera. Here the small weight of the animals necessitated a much more refined technique. This work is so recent that it is sufficient to mention the principle used. The weight of an insect depressed a counter-balanced treadle, completing an electric circuit through an electro-magnet, which in turn moved an inked pen which registered the animal's movements upon a moving drum. Unhappily such an excellent piece of equipment was neither described nor figured in the text, nor were the experimental conditions of the cellar, in which the experiments were conducted, fully described. The work, however, is the best that has been done with recording apparatus in measuring nocturnal activity.

Four years ago the writer began construction of a recording apparatus [1] which would measure objectively the activity of small animals. The circular disk of a phonograph, having a diameter of eleven and three-quarter inches, or No. 10 aluminum pan-covers, were threaded at the exact center so that a brass screw, which was lathed to a blunt point, could be inserted from above and adjusted to any required length. This screw point was centered on a dish-shaped table made by cutting off the end of another brass screw and

polishing the surface. This second screw was passed from below, through an oblong of transite measuring $16 \times 14 \times \frac{1}{4}$ inches. The latter was threaded to hold three brass screws so arranged that the transite base could be leveled rapidly, and secondly threaded for four brass screws so that their filed points would contact with the circular disk noted at the four major compass points (fig. 1a, b). A rim of celluloid, three inches high, was placed
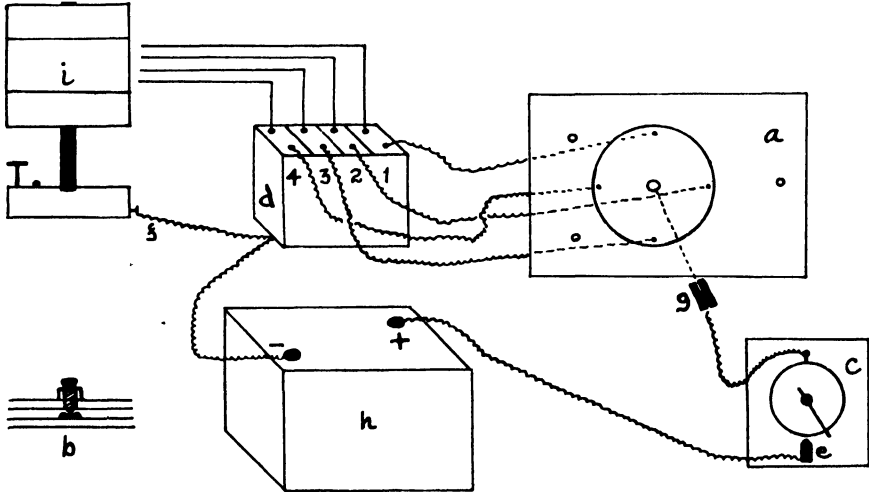


Fig. 1. Recording Apparatus for Measurement of Nocturnal Activity. *a.* Transite plate with three leveling screws, four peripheral contacts, and central contact on which is balanced a circular disk. *b.* Method of balancing circular disk on central contact. *c.* Electric clock. *d.* Model T Ford ignition coil. *e.* Mercury cup contact for sweep-second clock hand. *f.* Shorting wire from Kymograph back to coil. *g.* Fuse wires *h.* Six volt storage battery (or transformer if using alternating current). *i.* Kymograph drum mounted on 24-hour Taylor clock-works.

against the raised rim of the disk to complete a container for the experimental animals. When in use the transite base was leveled rapidly and the container or disk balanced so that it just cleared the four screw points, or lightly rested on one of them. The plate when balanced could be deflected by a gentle breath and was sensitive to half a gram.

The central contact of the base, upon which the disk is balanced, was wired to an electric clock (fig. 1c), and the four peripheral contacts wired respectively to four vibrators of a Model T Ford coil (fig. 1d), each of which bears a sharpened iron wire. The terminals of this coil are wired to the negative pole of a six volt storage battery, and the positive pole of the latter is wired to a cup of mercury (fig. 1e) so placed that a copper wire or strip attached to the sweep-second hand of the clock passes through the mercury for a fraction of each minute. The use of the storage battery is especially desirable for field recording but in the laboratory a transformer was wired to the coil and alternating current used.

One end of the primary circuit, then, is completed for a part of each minute by the sweeping second hand. The duration of this contact between clock and mercury cup is adjusted by manipulating either the length of the second-hand strip or the amount of mercury in the cup. I found between two and three seconds to be a desirable contact. The other end of the primary circuit is always complete as a consequence of the loaded disk touching one, or two adjacent, peripheral contacts. Each minute the circuit is made, and the coil wires of the secondary circuit fire a spark of roughly a quarter to a third of an inch long. These sparking wires burn small dots into a strip of adding machine paper which is fastened around a kymograph drum driven by a 24 hour Taylor clock-works. Thus a continuous record is formed, each minute giving the position of the contained animal on the disk, and hence its inactivity, and duration and direction of its active periods. The record is divided into twenty-four hour lines and the apparatus started at a given line. To prevent a spark from jumping through the record and metal drum and back into the passive sparking wires, the drum is shorted back to the coil (fig. 1f). Finally, if the electric clock should stop at the moment when the second hand was contacted with the mercury cup, the resulting continuous arc of one or more coil wires would set fire to the moving paper record. To avoid this danger, fuse wires totaling one and a half amperes were placed in the primary circuit (fig. 1g) and at this amperage a single contact of more than five seconds would melt the fuse and stop the sparking until the gap had been repaired.

Obviously, in analysis of activity rhythm as complete a control of the immediate environment as possible is necessary to a proper evaluation of the data obtained. To this end the disk holding the animals, and the supporting base were placed in a cabinet and the several wires running from the central and peripheral contacts passed through the wall of the cabinet to the recording unit which was arranged compactly outside. This cabinet has been previously described (Park and Keller, '32), but it may be said here that the air temperature, relative humidity and rate of evaporation within the cabinet were held practically constant, air movements were absent, and when closed the interior was in complete darkness. If desired, the interior of the chamber can be illuminated by directing a beam of light through an uncovered double glass port, the heat being carried away by a stream of water moving between the port and the light source. In using this chamber with a saturated atmosphere it became necessary to avoid rusting. To this end brass screw contacts were utilized and the transite plate did not warp, an event which would throw off the distance between the plate and the peripheral contacts. Also, the aluminum disks were used in such atmospheres rather than steel ones.

Like most apparatus, this one is far from perfection and has evolved from a very crude original machine. One of its chief faults is that, when the plate is balanced so that one animal in walking around its circumference progressively makes each peripheral contact strong enough to overcome contact

resistance, food or a part of the environment cannot be added as the plate would become unbalanced permanently for the experiment; even the accumulation of faecal pellets in certain species of insects over twenty-four hours would at times overbalance the disk. Hence an artificial environment must be reckoned with in interpretation of the data, and where starvation or muscular fatigue is not being investigated directly, short runs of twenty-four hours must be alternated with periods of rest in which the animals can eat and drink. With animals of a gram or more in weight, however, satisfactory records can be confidently counted upon. Under a gram, very light aluminum disks must be used and the transformer set at a much higher voltage to gain complete records.

Data taken with this apparatus in the laboratory can be supplemented by obtaining data in the field with a compact, duplicate unit, using the storage battery of an automobile, and a clock-works for the transformer, and electric clock respectively. The unit can be sheltered from falling leaves or strong winds by appropriate screens, and data compiled under normal habitat conditions. Further electromagnets drawing pens over the record can be used in place of the sparking coil, in either laboratory or field.

### Further Analysis of Nocturnal Activity

It was shown previously (Park and Keller, '32) that species active at night belonged to at least two categories, *viz.*, their activity apparently was largely controlled by the operative environmental factor complex (Environmental Type), or the activity was more or less inherently rhythmic and consequently apparently not affected by changes within the normal environmental limits (Inherent Type). Lutz ('32b) also found inherent activity in three more species of insects, using the Lutz recording apparatus mentioned earlier.

The work done by Park and Keller was subjective to the extent that change in position of marked individuals was measured by eye, and there was the further objection of illuminating the experimental chamber for a few seconds each hour. Although it was felt that the results obtained were sound, an objective check of the problem was necessary. The recording apparatus described in this article was developed therefore, and a part of the data taken with this instrument over the last two years are given at this time.

It has been rather difficult to acquire suitable experimental material due to the following limitations: (1) the species must be common enough to be obtained in relatively large numbers from its natural habitat; (2) heavy enough to strongly depress the suspended disk in the experimental cabinet (1 to 2 gms.); (3) flightless, or at least unable to escape from this walled-disk.

Data on two of those animals which were found to meet these conditions are presented here. These are the black passalid beetle, *Passalus cornutus*, Fab., and the milliped, *Spirobolus marginatus* (Say). Both species are rela-

tively large, heavy, hardy forms which are both abundant and characteristic inhabitants of decaying logs, especially of the more mesophytic forest floors.

## Results with Passalus cornutus

Individuals or colonies were taken from logs in a climax maple forest and their activity measured in the laboratory at once. They were then kept in fresh, moist log mold in the laboratory until needed for later experiments of the same kind to determine how resistant their activity cycle was to the change in habitat conditions.

The following table (table I) summarizes the results obtained in analysing activity cycles of solitary *Passalus cornutus*. The table is concerned only with the activity of single individuals for twenty-four consecutive hours, so that hunger and fatigue are minimized as much as possible. In part of the trials the cabinet was kept in the laboratory, and partly kept in a basement where the maximum summer fluctuation was only 3.3° C. Within the experimental cabinet the average temperature range was 2 degrees (22.6 to 24.6° C.), with a minimum 24 hour fluctuation of zero to a maximum of 3.5 degrees. The average rate of evaporation in the cabinet was 0.32 cc. per hour, with a minimum hourly rate of zero at saturation, to a maximum hourly rate of 0.44 cc. in other trials. The cabinet interior was in total darkness.

TABLE I. *Activity of single Passalus cornutus for 24 consecutive hours in total darkness*

| Date of trial | Animal | Trial | Experiment started | Total Activity in hrs. for 24 hrs. | Night Activity (6 P.M.– 6 A.M.) in hrs. | Day Activity (6 A.M.– 6 P.M.) in hrs. |
|---|---|---|---|---|---|---|
| 10–17–31 | No. 1 | 1st | 10:00 P.M. | 8.83 | 6.33 | 2.50 |
| 10–27–31 | No. 2 | 1st | 4:00 P.M. | 9.75 | 3.75 | 6.00 |
| 10–31–31 | No. 3 | 1st | 2:00 P.M. | 6.50 | 4.50 | 2.00 |
| 5–31–32 | No. 4 | 1st | 3:00 P.M. | 7.50 | 3.00 | 4.50 |
| 6– 4–32 | No. 4 | 2d | 8:45 A.M. | 3.25 | 0.50 | 2.75 |
| 10–19–32 | No. 5 | 1st | 11:30 A.M. | 11.25 | 4.50 | 6.75 |
| 11–10–32 | No. 6 | 1st | 10:10 A.M. | 8.33 | 3.00 | 5.33 |
| 1– 9–33 | No. 50 | 1st | 9:00 A.M. | 9.50 | 0.50 | 9.00 |
| 1–24–33 | No. 50 | 2d | 1:10 P.M. | 15.00 | 7.00 | 8.00 |
| 1–26–33 | No. 52 | 1st | 10:00 A.M. | 10.00 | 3.25 | 6.75 |
| 2– 2–33 | No. 51 | 1st | 9:05 A.M. | 7.50 | 2.75 | 4.75 |
| 2– 8–33 | No. 51 | 2d | 10:30 A.M. | 14.75 | 10.25 | 4.50 |
| 2–14–33 | No. 50 | 3d | 11:00 A.M. | 22.00 | 12.00 | 10.00 |

9 individuals in 13 trials for a total of 312 animal experimental hours.

| | | | |
|---|---|---|---|
| Total hours active: | 134.16 | Twenty-four hour average: | 10.32 hours |
| Night hours active: | 61.33 | Nightly active average: | 4.71 hours |
| Day hours active: | 72.83 | Daily active average: | 5.60 hours |

From this table we see that apparently time of year, time of start of trial, familiarity with apparatus as indicated by trial sequence, and interval spent in laboratory have little appreciable affect upon the character of the activity. As expected, some animals tended to give individualized behavior, as was indicated earlier for another beetle, *Patrobus longicornis* (Park and Keller '32).

The experimental conditions of darkness, constant moisture, temperature, etc., at least parallel the physical conditions obtaining in the natural log habitat. This is interesting in view of the chief conclusion reached, *e.g.* that *Passalus cornutus* has no definite rhythm or periodicity of activity. The daily activity is roughly 54 per cent, and the nightly activity is 46 per cent, of the total, and these averages are not applicable to all individuals. Therefore, in
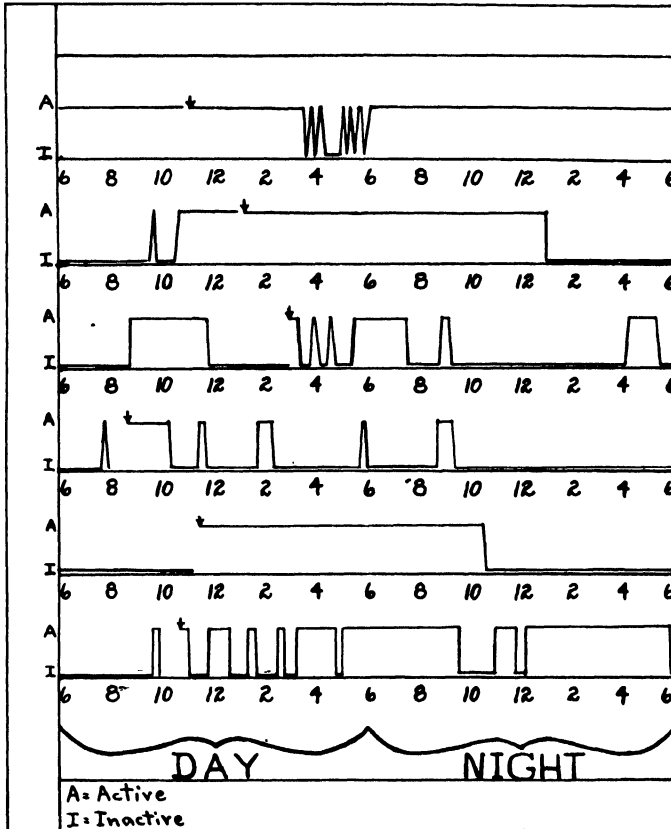


FIG. 2. Arhythmic Activity of Individual *Passalus cornutus* in Total Darkness. Temperature, humidity and evaporation rate practically constant. Arrows indicate start of each trial.

addition to the Inherent and Environmental types of activity rhythms, defined previously, we are led to postulate a third, or Arhythmic type. The following graphs (fig. 2) illustrate this third condition.

I find this arhythmic condition in *Passalus cornutus* especially interesting, since the passalids in general are equipped with a body of social " instincts," live in colonies and care for their young (*cf.* account of Ohaus in Wheeler ('23) ; Miller ('32)). Further investigation may show that the social spe-cies of insects, *e.g.* the ants, etc. have less inherently fixed rhythms of ac-

tivity than the solitary species. This has been indicated previously for ants (Park, Lockett and Myers, '31; Flint, '14), where individuals were apparently never all active at the same time, and there was a general absence of species activity rhythm. If this is true, the social habit may be advanced either as a possible outcome of the arhythmic condition, or as an underlying causal factor for the appearance of this aperiodicity.

On the other hand, the activity rhythm of a species may be wholly unrelated to the social matrix. If such is the case, this arhythmic habit may be viewed as a loss or impairment of an original inherent activity rhythm through time, since all stages of the life cycle of *Passalus cornutus* are passed within the dark, stable log mold save when adults move from one log to another.

### *Results with Spirobolus marginatus*

Turning to the millipedes, it was found earlier that under natural conditions, *e.g.* in the forest at night, they were nocturnal (Park, Lockett and
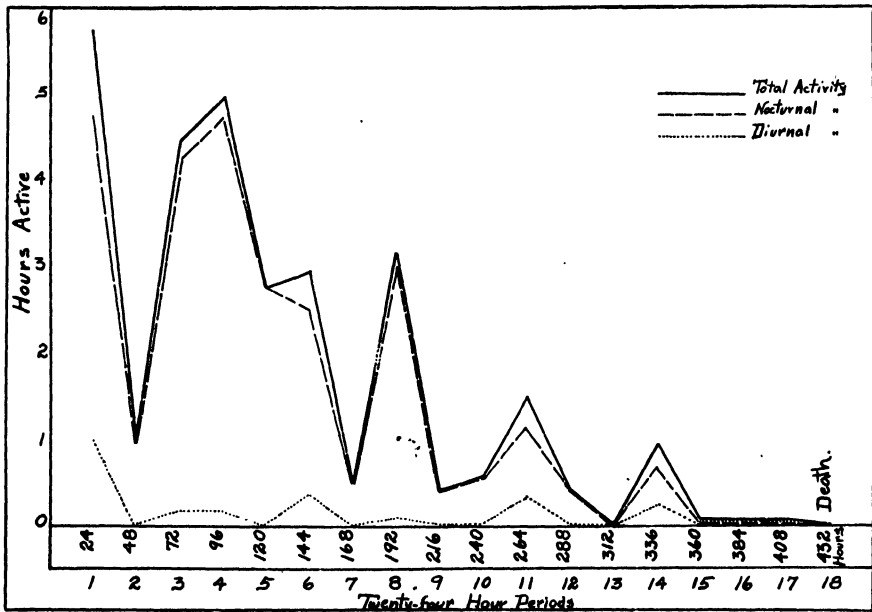


Fig. 3. Inherent Nocturnal Activity of *Spirobolus marginatus*. Showing relation of total, nocturnal, and diurnal activity in constant darkness, temperature and humidity to rhythm persistence, *vs.* starvation. Weight at start of experiment 1.50 grams; weight at death 0.86 grams. Note that for the first fifteen twenty-four hour periods the starving animal manifested 88 per cent of nocturnal activity as against 8.5 per cent of diurnal activity, and that the relative inactivity increased with increase of hunger and fatigue.

Myers, '31). The data taken on *Spirobolus marginatus* bear out these observations. Under the identical experimental conditions used in studying

*Passalus cornutus,* this species of millipede was rarely active by day and predominantly active at night. Therefore, *Spirobolus marginatus* has an inherent nocturnal rhythm.

After the innate nature of the rhythm had been established, individuals were allowed to remain in the experimental cage, without anything to eat or drink. As would be expected under such conditions, they lived from ten to eighteen days, with a gradual decrease in weight and activity. However, as shown by table II and figure 3, which summarizes a typical case, the general character of the rhythm did not change, the animals being preponderantly active at night.

TABLE III. *The effect of starvation upon the Inherent Nocturnal Activity of a Spirobolus marginatus until death (432 hours), under constant darkness. humidity, temperature and evaporation rate. Weight at start (3:00 P.M., June 28), 1.50 grams; Weight at death (3:00 P.M. to 10:15 P.M., July 16), 0.86 grams. (Hours = ';* *Minute = ")*

| Elapsed time in hours | Total activity per 24 hrs. | Night activity (6 P.M.–6 A.M.) | Day activity (6 A.M.–6 P.M.) |
|---|---|---|---|
| 24  | 5' 45" | 4' 45" | 1' 00 |
| 48  | 1' 00  | 1' 00  | 0 00  |
| 72  | 4' 25" | 4' 15" | 0 10" |
| 96  | 4' 55" | 4' 45" | 0 10" |
| 120 | 2' 45" | 2' 45" | 0 00  |
| 144 | 2' 50" | 2' 30" | 0 20" |
| 168 | 0 30"  | 0 30"  | 0 00  |
| 192 | 3' 10" | 3' 05" | 0 05" |
| 216 | 0 25"  | 0 25"  | 0 00  |
| 240 | 0 35"  | 0 35"  | 0 00  |
| 264 | 1' 30" | 1' 10" | 0 20" |
| 288 | 0 25"  | 0 25"  | 0 00  |
| 312 | 0 00   | 0 00   | 0 00  |
| 336 | 0 55"  | 0 40"  | 0 15" |
| 360 | 0 05"  | 0 00   | 0 05" |
| 384 | 0 05"  | 0 00   | 0 05" |
| 408 | 0 05"  | 0 00   | 0 05" |
| 432 | 0 00   | 0 00   | 0 00  |

Total Experimental Hours: 432
Total Inactive Period:      402' 45"
Total Active Period:         29' 15"
Total Night Activity:        26' 10"
Total Day Activity            2' 35"
(Including adjustment period of 30 min. activity at start of experiment). .

Thus in the experiment graphed, of a total of 432 hours spent in the dark experimental chamber, roughly 88% of the activity of the starving animal was at night, and 8.5% during the day. Hence we are led to believe that their innate activity is a deep-seated mechanism.

From this graph we also find that the general activity rises and falls, on the average reaching a maximum every second night, until the very end of the experiment when exhaustion made any but the smallest movements

impossible. We suggest that these peaks of activity represent more or less normal periodic searching for food, which gradually decrease in strength and duration as fatigue increases.

### SIGNIFICANCE OF RHYTHMIC ACTIVITY TO CERTAIN PROBLEMS

Before the writer began studying nocturnal animals, he held a too generalized concept of protoplasmic response to environmental stimuli. The literatures of experimental physiology and development gave innumerable examples of the modifiability of response, and within the confines of ecology, it was obvious that such phenomena as aggregation, hibernation, and others could be controlled by certain techniques. From such a position it was easy to assume that, granting a peculiar genetic matrix, the autecology of any species was a series of responses, called into being by internal states but strictly under the control of the environmental complex. Now if this was applied to the study of distribution and activity of an animal community, the well known limiting and modifying affect of the external physical factors was realized, and justifiably so. However, the complete activity-inactivity cycle of the species involved was also considered a product of the environment. Apparently, in view of the recent work on nocturnal activity, this last tacit assumption was unjustifiable.

In other words, the very existence of periodic active and inactive states was confused with the environmentally modifiable rate and character of these states. Persistent activity rhythm in darkness was found in forest deer mice (Johnson, '26), a species of *Microtus* (Davis, '33), three species of Orthoptera (Lutz, '32), a beetle, *Boletotherus cornutus* (Park and Keller, '32), and the millipede, *Spirobolus marginatus* reported here. In all seven of these species (embracing rodents, millipedes and two orders of insects), a dark, constant environment did not prevent the animals from being more active at night than during the day. It is to be expected that this rhythm would break in time due to the increasing fatigue, although in the case of *Spirobolus marginatus* this seemed unusually long delayed. Where the illumination was reversed, the rhythm was reversed in all save one species. This reversal does not disprove the innate nature of the cycle; rather it shows us that the rhythm can be experimentally modified. The rate and character of the reptilian heart, to cite another example, can be controlled by experimental technique (Chu and Sollmann, '25 a, b), yet the innate nature of the cardiac rhythm is apparent. Neither does it clarify the problem to term such periodic activities habits or instincts. To this end, critical study of the affects of each operating factor and combination of factors should further our knowledge of nocturnal activity.

It would appear axiomatic that, since certain species have been shown to be active despite controlled environment, too many conclusions have been drawn in the study of activity, or its results in ecological communities, especially with reference to the data collected on physical environmental factors.

In studying nocturnal animals, Park, Lockett and Myers ('31) found the environmental data paralleled animal activity. One of the species studied at that time was subsequently observed under controlled conditions in darkness (Park and Keller, '32) and this form, *Boletotherus cornutus,* gave the same nocturnal rhythm. In the first paper environmental control was the apparent explanation, although internal rhythmicity was realized to be a possibility; in the second paper, the data showed the activity to be an expression of inherent rhythm within the limits of the experiments. Another species, *Parcoblatta pennsylvanica,* studied under the same controlled conditions, was found to have its activity far more amenable to environmental manipulation. From this it appears unsafe to draw conclusions as to the cause or nature of population activity or movements within a community, unless at least the characteristic species have been thoroughly studied experimentally to determine the type of activity rhythm they manifest. A great amount of autecological work is indicated.

Future investigation may find that the several types of nocturnal activity noted here are quantitative concepts only, and hence the necessity for types of rhythm may eventually disappear. Naturally, the degree of inherent and of environmentally-induced activity is important as bearing upon the ageless problem of heredity and environment. Further, in species which may have inherent rhythms, there lies the further problem of the nature of the control, *e.g.,* whether genetic, hormonal or both. The rhythm in the movement of eye pigment of several species of crustaceans recently demonstrated (Bennitt, '32; Welsh, '30) bears on this problem, and a vascular regulation is suggested by these authors, following the results of Perkins ('28), and Perkins and Kropp ('32).

The body temperature rhythm is obviously closely related to activity in warm-blooded animals, and analysis of temperature rhythm in both warm- and cold-blooded species has just begun. Hilden and Stenbach ('16) are said to have confined birds in a dark room and to have regulated activity by artificial light, and to have reversed the temperature cycle. Wetmore ('21) and Simpson and Galbraith ('05) found diurnal and nocturnal species to have directly opposite curves of body temperature, each type paralleling the respective active and inactive periods. Wetmore is probably correct in thinking this rhythm a result of metabolic activity, although this is in turn partly a result of bodily activity. However the question arises to what extent, if any, is this species activity inherent, and to what extent environmental. Further, inherent temperature rhythms may be looked for, even in cold-blooded animals. Far more exact methods and controlled experiments are needed to investigate this group of problems. .

Following analysis of activity, we will be much nearer an appreciation of population curves in community studies. As yet no study in total nor stratal population for nocturnal animals is available, and the structural ad-

justment of nocturnal species is very incompletely known (*cf.* literature cited by Park and Keller, '32; Crawford, '33 a, b, '34; Walls, '31).

To what extent the nightly active species prey upon their fellows, and upon resting diurnal forms is also relatively unknown (Elton, '32). Clark ('14) has suggested that the predative mammals and birds, which are largely nocturnal, feed chiefly upon sleeping diurnal species, in fact owe their nocturnalism to this ecological arrangement. Finally the origin of the nocturnal habit is quite unsolved and both Clark ('14) and Kennedy ('28) have interesting suggestions upon this point.

## SUMMARY

Three types of recording apparatus for measuring nocturnal activity are discussed briefly, and one of these described in detail.

An arhythmic form of activity is described for *Passalus cornutus,* and a possible bearing of this upon the social habit is noted. An *inherent* activity rhythm is described for *Spirobolus marginatus,* and the relation of this innate activity to progressive starvation is discussed.

An attempt is made to integrate partially a number of ecological and physiological problems on the basis of activity, and the bearing of data on nocturnal rhythms upon current community analysis is suggested.

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# STUDIES IN NOCTURNAL ECOLOGY, IV.
## *MEGALODACNE HEROS*

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### INTRODUCTION

The mycetophagous erotylid beetle, *Megalodacne heros* (Say), was observed to be active at night and inactive by day in its normal forest habitat by Park, Lockett and Myers ('31),. Since this species was nocturnal, relatively heavy, not given to prolonged flight, and was abundant in our neighboring forests, its activity could be measured by recording apparatus described previously (Park, '35), as well as observed in the field. Therefore a series of experiments was outlined to throw light upon the activity of this species, a part of which is reported here in condensed form. Part of the work was done with marked individuals under natural conditions and part in the laboratory under controlled, constant conditions; both phases of the program tended to check and evaluate each other.

### RESULTS WITH MARKED INDIVIDUALS IN THE FIELD

A small log, six feet long by eight inches in diameter was selected. The log was soft with decay throughout (stage 4 of the log decay cycle) and held a variety of fungi. Flaps of bark were attached at several places to the log and twenty fresh shelf fungi (*Fomes applanatus*) were nailed on to increase both the food supply and available habitat niches. To allow ready examination of the lower surface the log was placed across two uprights, two feet above the floor. Both wood and fungi were kept moist by thorough watering once each day or night, at varying times through the progress of the work, and the log was so placed that two-thirds was always heavily shaded during the day.

After trying various paints and lacquers, it was found that Baer's Aluminum Paint gave conspicuous and enduring results. The beetles were then marked differentially and placed on the log. After several hours adjustment, regular hourly readings were taken, on the hour, to determine the position of the animals each reading. By using a small mirror the individuals in or under a niche could be located without disturbing them. At night, readings were taken by the dim light of a flashlight with its bulb coated with red ink. Each fungus, bark flap, crack, *et cetera,* was given a niche number and the distance between any two niches could be rapidly and accurately measured. The readings, therefore, gave information as to the change of

position on the log, and the minimum hourly distance moved for each experimental animal. After a period of orientation, regular readings were begun for trials varying from 24 to 96 consecutive hours with varying numbers of the same or new individuals. From seven to thirty animals were usually used and these were (1) taken direct from the forest in some trials, (2) or placed on the log after having been used in the recording apparatus, (3) or taken from a two weeks confinement in light-tight tins in a basement.

For practical purposes dusk was fixed as the first reading at which the flashlight was necessary to locate the marked beetles, and dawn the first reading which could be taken without the use of the flashlight. Using these conventions, for the period of the field work (July) dusk fell at the 8:00 P.M. and dawn at the 5:00 A.M. readings. This gave a nine hour night and a fifteen hour day.

*Autecology of Megalodacne heros* (Say). Regular observations of the beetles gave many data on their behavior. They spent the day in an inactive state, or moving very slowly for short distances within the habitat niche. Of the many shelters provided only seven were consistently occupied each day, and these few usually held from three to six individuals. Promptly at dusk the beetles moved from their niches to feed upon the fungi. Although they fed on *Fomes applanatus* to some extent, most of the feeding was done on a small patch of soft, velvety fungus some six inches long by two inches wide on the lower surface of the log. The species is nonspecific in its choice of fungi as it was observed eating a species of *Pezizia* at 9:18 P.M. (Park, Lockett and Myers, '31), and is commonly found upon species of *Polyporus* (Dury, '18; Weiss, '20; Park, '31), and other fungi.

Collection and observation in the field for the past ten years has shown that the species aggregates regularly, either in fungi or under bark or decaying wood near fungi. In the first case the niche was serving both as food and shelter, in the latter cases as shelter only, this niche being from several inches to twenty-five or more feet from the nightly feeding grounds. Such gatherings are essentially "shelter aggregations" formed by crowding, although since all the available space is not occupied, the gathering may not be wholly explained upon the factor of overcrowding (Allee, '27; Park, '30). Such gatherings were passive, the aggregants usually resting quietly in contact with others, or at times piled one on top of the other, in a small area, three or four deep.

During July, copulation was frequently observed (table I). Although this occurred as early at 8:00 P.M. (dusk) and as late as 6:00 A.M. (one hour after dawn), copulation was more frequent after midnight, especially between 1:00 A.M and 4:00 A.M. Of the forty odd individuals observed in general, not all copulated. Rather a relatively few beetles tended to copulate a great deal, a fact ascertained only by using marked animals.

In one case, before copulating a male and a female faced each other and each brushed the log laterally with their fore-tarsi, in rapid movements as

though digging.  In copulation the male normally mounts the female directly
from the rear, climbs to the latter's elytra and clasps them firmly with the
mesothoracic legs, the metathoracic legs being used as accessory clasping
organs, or trailing limply behind.  The male's intromittent organ is exserted
slowly, curved downwards and usually inserted from the left side into the
female's genital pore.  After insertion of its apex, the abdomen of the
female is extended rapidly posteriorly and envelopes the intromittent organ.

TABLE I.  *Copulation in Megalodacne heros*

| Date | Time | ♀ Individual | ♂ Individual | |
|------|------|-----------|-----------|---|
| July  8 |  9:40 P.M. | Control | Control | |
| July 10 | 10:30 P.M. | Control | Control | |
| July 12 | 10:30 P.M. | Control | Control | |
| July 14 | 12:00 Midn. | No. 2 | No. 6 | |
| July 15 |  1:00 A.M. | 2 | 6 | |
|         |  3:00 A.M. | 2 | 6 | |
|         |  4:00 A.M. | 2 | 6 | |
| July 20 |  3:00 A.M. | 17 | 23 | |
|         |  4:00 A.M. | 17 | 23 | |
|         |  8:00 P.M. | 17 | 23 | |
| July 21 |  4:00 A.M. | 17 | 23 | |
|         | 11:00 P.M. | 22 | 21 | |
| July 22 |  1:00 A.M. | 22 | 21 | |
|         |  2:00 A.M. | 22 | 21 | |
|         |  3:00 A.M. | 22 | 21 | |
|         |  5:00 A.M. | 22 | 21 | |
|         |  6:00 A.M. | 22 | 21 | |

Although the male is usually exactly placed dorsal in position, he may
be displaced either on the right or left elytron of the female at times.
Once one female was seen copulating with two males simultaneously, each
placed symmetrically upon one elytron, and each with the intromittent organ
inserted well into the female genital pore.

Copulation is usually lengthy, although sometimes the male is brushed
off by the female after several minutes, a pair may copulate for hours or
several times during a night.  The female is usually active during this
period, walking and feeding upon the fungi while the male is passive, clasping
the female and slowly moving the prothoracic legs and antennae, as is the
rule for many species of beetles (*e.g., Harpalus caliginosus, Chlaenius,* etc.).
However upon one occasion the male was quite active in the following manner:
at intervals of about half a minute the prothoracic legs were vibrated very
rapidly in a vertical plane and then brought down diagonally so that the
brush of orange colored pubescence on the tarsi grazed against the lateral
margins of the female's pronotum.

*Nocturnal Movement under Natural Conditions.*  Although certain forms
of activity were more in evidence after midnight, most movement came at
dusk.  In the following graph (fig. 1) the minimum distance moved in inches
per hour for thirty marked individuals is shown for 216 hours under field

conditions (2160 animal hours). From this typical curve it is obvious that *Megalodacne heros* shows a crepuscular tendency, remaining inactive through the day within the shelter niches and moving to the fungi when
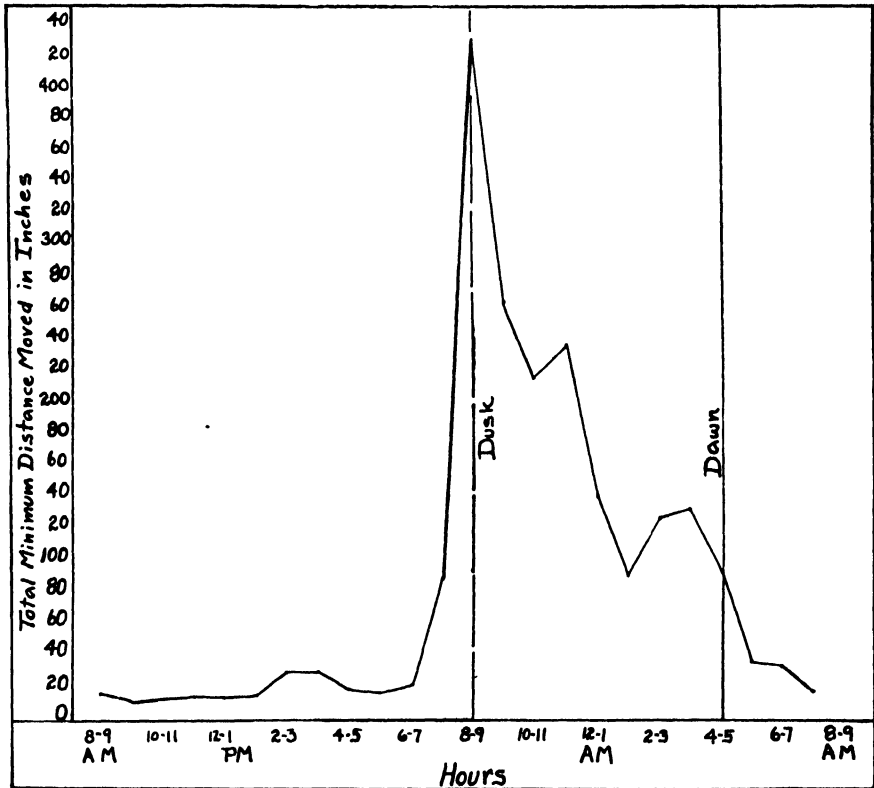
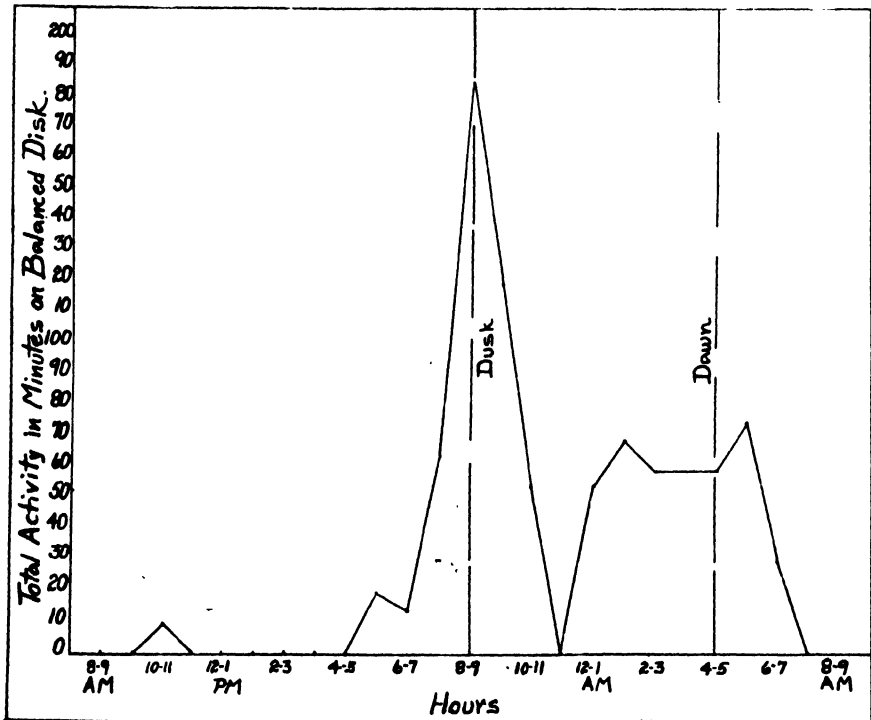

Fig. 1. Nocturnal Activity of Megalodacne heros under natural conditions. Combined total activity of thirty marked individuals for nine days and nine nights (216 experimental hours = 2,160 animal experimental hours).

the sun has set. This dusk activity is a mass movement of virtually all of the individuals to the feeding areas. After dusk feeding continues for some time. Some of the beetles fed for several hours at a time and then moved to a shelter niche for the duration of the night. Others fed for much less time, retired to shelter and then moved out to feed again near the middle of the night and again at dawn. Some fed each night, others every second night, but the tendency was to feed at dusk for about an hour, retire and come out again for one or two times as indicated in the lesser peaks in the curve. This gradual falling off of activity, measured in terms of movement per beetle-hour, approached zero at dawn, when the large majority of the animals had retired for the day.

## RESULTS UNDER CONTROLLED CONDITIONS

*Method.* Data collected in the field indicated that the nightly activity appeared to be in close correlation with the operative factor complex. Previous experience, however, in the case of another fungicole (*Boletotherus cornutus,* Park and Keller, '32), suggested that the correlation might be apparent rather than real. Consequently, the same marked individuals were placed under constant environmental conditions and their activity measured by the recording apparatus noted previously.

Individuals of known behavior were studied first separately, and then *en masse,* to determine (1) to what degree the rhythm of nocturnal activity was innate, and (2) the effect of aggregation upon activity. In both sets



FIG. 2. Inherent Nocturnal Activity of Megalodacne heros under constant Conditions. Combined total activity of ten marked individuals in recording apparatus for ten separate twenty-four hour experiments (240 experimental hours = 240 animal experimental hours). Total darkness; cabinet air temperature 23.9 to 25.3° C.; rate of evaporation 0.20 to 0.30 c.c. per hour. One individual in each experiment.

of experiments the animals were in total darkness, the air temperature of the cabinet had an extreme limit of variation of from 23.9 to 25.3° C., with a constant rate of evaporation of 0.20 to 0.30 c.c. per hour for the duration of any experiment. Neither food nor water was supplied in the cabinet, but

between trials the animals were given fresh fungi in a dark, moist container so that hunger and fatigue were eliminated as much as possible.

The graph (fig. 2) sums up the results obtained with isolated beetles for trials of 24 consecutive hours per trial. It will be seen that the periodicity was maintained, the peak of activity coming suddenly at dusk when in nature the species normally leaves its shelter for food. Again, this activity was of the same duration as in nature. After the initial period of activity the beetles were more inactive than when under normal conditions. However, both minor peaks were indicated, the normal midnight rise falling about two hours later, and the normal pre-dawn peak also coming about two hours later. Thus the character of the rhythm was maintained, *i.e.*, the nocturnal behavior was largely innate, but after the dusk migration, the animals tended to be less active.
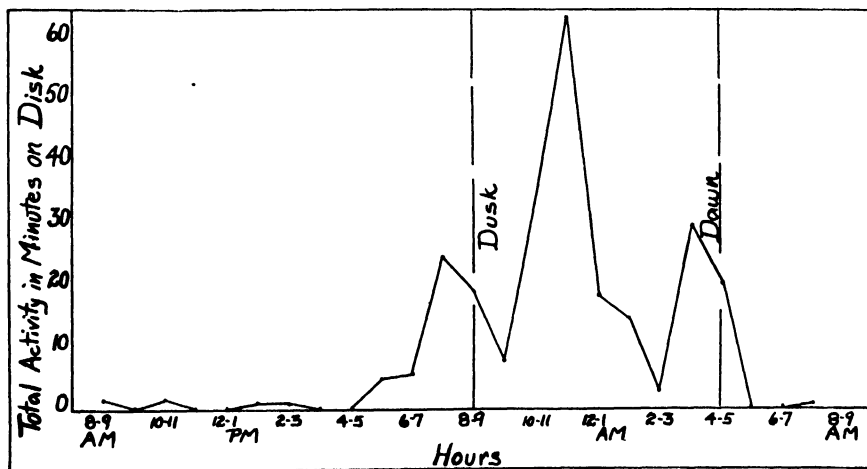


Fig. 3. Effect of Numbers of Individuals upon Inherent Nocturnal Activity. Combined total activity of twenty-eight marked individuals in recording apparatus under the same conditions as listed in figure 2, as follows: Nos. 1–7, 16, 20–22 (11 individuals for 72 consecutive hours) ; Nos. 25–31 (7 individuals for 72 consecutive hours) ; Nos. 25–34 (10 individuals for 24 consecutive hours). 168 experimental hours = 1,536 animal experimental hours.

To test the effect of numbers upon amount of activity, the same beetles were placed in the apparatus under the same physical conditions, but in groups of from seven to eleven individuals. The graph (fig. 3) shows the effect of numbers of animals. A comparison of figures 2 and 3 makes clear that (1) numbers of individuals do not eradicate the innate behavior, but (2) do reduce the amount of activity to roughly one-third that of solitary forms, and (3) apparently alter the character of the nightly movement. It has been abundantly demonstrated elsewhere (Allee, '27, '31) that numbers tend to reduce activity in certain species of animals and under certain con-

ditions, so that the second conclusion given above is not wholly unexpected. However, the slowing down of group activity taken in conjunction with certain shifts in the rhythm pattern is more interesting. It would appear that the grouped beetles continued to have a nightly activity with three peaks, but all of the peaks are from one to two hours earlier, and secondly, the maximum falls at about midnight for groups, as opposed to a maximum at dusk for isolated animals experimentally controlled and under natural conditions.

It may be added here, in justification of the technique employed, that the correct interpretation of the data under laboratory conditions was only possible in the light of normal activity studied under field conditions, so that both sets of data tended to clarify the problem when viewed as a whole. A great deal of conjecture could be utilized to interpret the nature of the changed rhythm of groups of the beetles but we feel that little more than presentation of data is permissible at such an early stage of investigation. Certainly poor physiological condition of the experimental animals may not be advanced as the beetles were well fed with their normal food, and kept in dark, roomy, humid containers. Thirty-two of the thirty-four animals used remained normally active at night, feeding and copulating for three months after the experiments were finished. This is significant for this species as it is susceptible to adverse conditions. Starvation or over-stimulation usually proves fatal in from seventy-two to ninety-six hours, while in other animals tried previously (*Spirobolus marginatus*, etc.), death did not come before two weeks in total darkness without food.

## Effect of Certain Factors upon Nocturnal Activity

There is a certain amount of evidence to indicate that the nocturnal activity of rodents, (*Epimys norvegicus albinus, Apodemus sylvaticus, Microtus*) is partly a result of hunger drives (Richter, '27; Elton, Ford and Baker, '31; Davis, '33). On the other hand, the milliped (*Spirobolus marginatus*) starved to death without fundamental change in its inherent nocturnal rhythm (Park, '35).

In certain beetles which aggregate in nature (*Megalodacne heros, vide supra*) the amount of total activity is reduced and the distribution of activity maxima altered at night when groups of individuals are studied under constant conditions.

Among physical factors it is natural that intensity of illumination should have been most thoroughly investigated in nocturnal animals. In a constant, dark environment the forms having an environmentally controlled rhythm (*Parcoblatta pennsylvanica*) so far have given a maximum response until fatigued, as would be expected (Park and Keller, '32); those species with no discernible rhythm of activity (*Passalus cornutus*) are not appreciably affected (Park, '35); finally, those species with a more deeply seated or

inherent rhythm of activity (*Peromyscus, Microtus, Gryllus, Stenopelmatus, Spirobolus, Boletotherus, Megalodacne*) are not appreciably affected by the darkness (Johnson, '26; Lutz, '32; Park and Keller, '32; Park, '35), their activity following the normal trends, other conditions being optimal and relatively constant.

However, within this last type of rhythm the species concerned vary in their pattern and degree of fixity of rhythm. In general, these preliminary studies tend to show that the invertebrates have more deeply seated activity rhythms than the rodents, the only group of vertebrates so far investigated. *Microtus* may be exceptional, however, since twenty-four days in darkness, but with proper food, failed to break the nocturnal periodism (Davis, '33). The latter author has suggested that such general activity may be correlated with photoperiodicity.

Experimental reversal of illumination reversed the activity rhythm in *Peromyscus* and *Gryllus*, but in *Stenopelmatus* the results were unsatisfactory as one of the individuals did not show reversal of rhythm (Johnson, 26, Lutz, '32).

## SUMMARY

From these observations it appears that (1) there are three forms of nocturnal response: environmentally controlled activity, inherent activity and arhythmic activity. (2) That although activity may be roughly allocated to one of these types of response, the character and requirements of such activity are species specific, as is shown by the differential response to the three factors so far investigated, *e.g.*, food, numbers of animals, and illumination. (3) That much work remains to be done in investigating the exact role of illumination, temperature and moisture.

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# PEAT LAND AS A CONSERVER OF RAINFALL AND WATER SUPPLIES [1]

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Over twenty years ago McGee ('13) of this Bureau published records of water levels in wells and subsoils. The data indicated a lowering in ground water levels in most states at a considerable rate since the settlement of the country. Among the causes for the general lowering of water levels, it appeared that changes in rainfall are not to be regarded as effective as the loss of water attending drainage operations and clearing, through surface run-off, and the increasing consumption of water by industries.

The influence of peat deposits as a combination of factors that conserve water is of great significance to scientific and economic interests. Peat land may be regarded as the longest recognized instance of the effects produced by relatively stable units of vegetation such as marshes, bogs, and forests. The retaining of water supplies in peat land distributed over arable land in the interior sections of the country, on watersheds, along streams and in valleys and plains constitutes today a vital problem. A critical statement of this subject should be helpful in considering the direct value of preserving peat areas, not so much in the light of a productive future source of organic material for soils, or of crops, pasture, and timber, as for state and national uses. Of the highest practical value is their protective function in conserving precipitation, storing water supplies, checking floods, erosion and silting, and maintaining a sufficiently high water table in surrounding land.

## PEAT LAND IN RELATION TO ATMOSPHERIC CONDITIONS

It is well known that physiological processes, which accompany plant growth, lead to evaporation of water from the leaves. Thus the relative atmospheric humidity is increased while the temperature of the air and that of the soil is reduced under a vegetation cover. Experiments on the amount of dry organic substance formed by crops show that corn, for example, evaporates about 300 units of water for every unit of dry organic material produced, and that an acre may yield approximately 7 to 8 tons of dry substance. Forests are reported to contribute in a larger degree than food or forage crops to the moisture content of the air and the consequent cooling of the atmosphere. Undrained peat deposits, whether in the form of bogs in which sphagnum

[1] The new program of conservation and land use has attracted attention to drained submarginal peat land and to a consideration of the general objectives appropriate to a national peat land problem.

mosses play an important rôle, marsh, or swamps covered by forest trees or shrubs, exert this influence in a much greater measure than crops. The cover of native vegetation is only one of the factors of conserving rain and snow, condensing fog and dew on the foliage, reducing any movement of water and mineral salts, and preventing the menace of silting. Organic soils are non-conductors of heat and surface layers of undrained peat areas exert, there-fore, a greater absorbing, condensing and cooling influence than mineral soils or rock with or without vegetation.

The effect of small peat areas upon local atmospheric conditions is, no doubt, small as compared with the effects of extensive areas of peat, such as occur in Florida, California, Minnesota, Wisconsin or Michigan. This con-clusion applies, of course, only to the influence of areas of peat that are in a more or less natural condition, but does not apply to conditions which arise from drainage, clearing, or destruction by fire. While definite observations and measurements are still lacking, there are several considerations that point strongly to a greater loss of water by evaporation from a bare or cultivated peat soil than from a water surface, to shrinkage and compaction, and to dis-tinct liability of fires, frosts, wind erosion, and excessive salt accumulation during any month of the growing season. Naturally the destructive effects on completely or even partially drained peat land in states within a sub-humid region or in a semi-tropical climate are much more serious than those from drained or bare peat land in the eastern, humid portion of the United States.

## Peat Land in Relation to Ground Water Conditions

The rainfall over a bog, marsh, or swamp forest is absorbed partly by the growing vegetation, but most of it penetrates into various kinds of peat below the surface. Absorption and retention of water vary with the kind of peat or muck and with the number and arrangement of the different layers that constitute the profile section of a peat area. The amount of water which is left over and above that lost by the growth and transpiration of the vegetation cover, and that held firmly by organic matter, increases underground and lateral seepage and becomes available as a supply for mineral soils, springs and streams.

Undrained peat areas in a level country show practically no run-off. Water and solutes do not move readily through accumulations of plant re-mains. Rainfall is in excess of the water loss by evaporation and the trans-piration of vegetation, and consequently sufficient water is retained to cause a general rise of the water table and a tendency to swell and float layers of peat and their surface vegetation. On watersheds, in hilly and mountainous re-gions, the surplus water in peat deposits, as that of forest-covered mineral soils, is one of the main sources of springs and stream flow.

Many experiments have been carried on in different parts of the world to determine the amount of water absorbed by various kinds of peat and muck

at the point of complete saturation.   The results obtained vary considerably with the character of the peat, its degree of decomposition, and the structural features of the profile of the respective peat area.

These facts are clearly brought out by investigations of the Bureau of Chemistry and Soils (Feustel and Byers, '30; Dachnowski-Stokes, '33). Peat materials consisting of colloidal organic sediments, woody residue, and fibrous plant remains, either from a network of reeds and sedges or from the entire plants of sphagnum mosses, differ widely in their ability to absorb the water received as rain or melting snow.   Figures obtained from a series of tests indicate that moss peat, when saturated, may contain 20 times its weight of water, swells, and under certain natural field conditions such as exist in raised bogs or " high moors " in Maine, water is raised in large amounts to a level 15 to 20 feet above the general surface. Fibrous, poorly decomposed reed or sedge peats contain only 7 to 6 times their own weight of water respectively.   To ascertain the actual amount of water absorbed in a given area by moss peat and by reed or sedge peat a calculation has been made based on the average volume-weight of organic material in pounds per cubic foot.   Moss peat is found to have an absorptive capacity of approximately 5200 tons of water per acre-foot of dry matter; reed and sedge peat have an absorptive capacity of approximately 4100 tons and 3500 tons respectively.   These quantities of water amount to a volume of 167,000 cubic feet per acre for moss peat and 131,000 and 112,000 cubic feet for reed and sedge peat.   The values are equivalent to a rainfall of 46 inches, 36 inches, and 31 inches respectively, indicating that under conditions of heavy or prolonged rainfall, the absorbing and retaining capacity of peat areas plays an important part in the storage of water and in mitigating severe and destructive floods.

The available information on the influence of forests upon ground water and stream flow is comprehensive (see Zon, '27).   There is, however, considerable divergence of opinion on the extent of this influence and the reliability of the data.   The effect of surface vegetation on stream flow varies with environmental conditions, and the amount of water discharged by streams is affected not only by the height and frequency of flood waters, but also by the rapidity of the stream flow.   Scientific methods of studying the relation of forest vegetation to stream flow have not been followed very long, and any attempt to base conclusions on inexact records has led only to confusion.   In the opinion of hydrologists and foresters alike, it is very necessary to carry on intensive observations on the actual discharge of rivers in selected, comparable watersheds that have a cover of forests or other vegetation, in order to justify important inferences.

Although few actual measurements have been recorded of the flow of waters from swamp forests, bogs, or marshy peat land, the data cited above establish with sufficient accuracy the conclusion that natural areas of peat, covered with native vegetation, whether located in cool, temperate, or sub-

humid regions, absorb precipitation and store more water than mineral soils. These conclusions cannot, however, be generalized for all kinds of peat areas. Deposits differ in depth, character and arrangement of different layers, in land relief and underlying mineral material. These and other factors also have a bearing upon the amount of moisture absorbed and retained but there is little doubt that peat areas are water reservoirs of the greatest importance.

Deposits of peat in regions of level character save more water and convey more water to the ground than forests, for as a matter of fact, forests consume more water and draw moisture from greater depths below the surface than any other type of vegetation; on account of their excessive transpiration they are known to lower the ground water level and to act as desiccators of mineral soils.

Peat deposits on watersheds and in mountainous regions, where erosion is easiest, receive more precipitation within certain limits of elevation than those at lower altitudes. They have an even greater influence in retarding the melting of snow and lessening the severity of run-off, erosion and silting. The denser the cover of natural vegetation, the smaller is the loss of precipitation water, partly through the interception by plant communities but largely, however, because the lower temperatures reduce evaporation and retard the decomposition of the constantly accumulating additions of organic matter that absorbs water. The ability of peat areas to conserve water supplies is greatest when peat profiles show transitional stages of development, that is, contain coarse, fibrous and porous grades of peat which permit a much greater percolation than maturer profile stages that have a surface layer of woody peat with a litter of leaves or needles of comparatively small water-absorbing capacity. Another important influence, often entirely overlooked, is due to the fact that peat materials, being poor conductors of heat, do not freeze to the bottom. Most of the peat land in the United States remains unfrozen at about a foot or two below the surface, thus keeping up an underground supply of available water nearly throughout the entire year.

To exercise their most beneficial effects in regard to water conservation, areas of peat land should, therefore, not be burned over, drained excessively, or otherwise interferred with in their normal development and protective function.

## FURTHER ASPECTS OF THE PEAT LAND PROBLEM

The geographic distribution of wet land, submarginal and unfit for crops without drainage, is shown in the U. S. Department of Agriculture Year Book for 1923 (p. 425); it aggregates over 100,000,000 acres and includes areas mapped as " peat and muck " and " marsh and swamp." Much of this land has been made economically unprofitable by unrestrained drainage, heavy expenditures for machinery and fertilizers, and serious crop losses from frosts, drought, wind erosion and fires. It is recognized that steps must be taken to determine the character of the nation's peat land, the purposes for which

these resources are best suited, and the practical measures that are required to re-establish natural conditions and protective functions. In the interests of a more permanent solution of the peat land problem, especially bogs, swamp forests, and marshes with receding water levels on watersheds and near streams and lakes, should be returned to long time use under the National and Recreational Parks Service, to Flood Control Projects, the Forest and Erosion Service, to game and wild life. .

A wise use of peat land resources is intimately related to the future of agriculture and the commercial utilization of peat products (Dachnowski-Stokes, '34).

In considering the direct value of peat land to water supplies and the need of conserving precipitation, American peat deposits may be placed into three major zonal groups and further subdivided into minor groups representing more or less definite combinations of physical features, land relief, drainage, and vegetation (Dachnowski-Stokes, '33).

The three major zonal groups are (1) the northern group of peat land with an abundance of moisture; (2) the central continental group with a fluctuating and unstable moisture supply; and (3) the group of southern and western peat land with insufficient moisture or a periodic water supply.

The problem of water conservation in each of these major groups is naturally different. In a general program of utilizing peat areas as water resources and obviating harmful effects, the plan should include a general reconnaissance of water-shed provinces, and the correlated factors that limit the use of peat areas in a constructive scheme of water economy or for other national objectives. Retiring large tracts of submarginal peat land offers an opportunity for conserving safeguards against drought, floods, erosion and lowered ground waters and for restoring the activity of natural vegetation as a constructive factor in the nation's land and water problems.

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# ROOT SYSTEMS IN ILLINOIS PRAIRIE [1]

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Only a very little of the work done on the extent of root systems of plants under field conditions deals in any way with that part of the United States east of the Mississippi River. A review of the literature indicates three papers concerned with the roots of native vegetation in the eastern part of the United States; those of Sherff ('12) dealing with swamp plants in the Chicago region, Waterman ('19) in the sand near the southern end of Lake Michigan, and Harshberger ('16) in the New Jersey pine barrens. In addition to these, others by Partridge and Veatch ('32) and Laird ('30) deal with the roots of cultivated crops. None of this work, however, is comparable with that of Weaver, Cannon, Jean, Crist, and others in the western prairies, plains and deserts. This lack of published information stands in marked contrast to the agricultural importance of this part of the country.

The prairie region of Illinois offered unusual opportunities for the furtherance of these studies, due to a similarity of the vegetation with that on which extensive studies have already been made and due to the agricultural importance of the area. The fact that no native prairie nor native prairie conditions now remain in this region should not impair the value of any results obtained, but rather should enhance them if these results are considered in relation to their present environment.

Among the most important early papers on the extent of root systems are those of Goff (1883, 1884, 1886), who was the first to make an extensive study of the subject. This work was done at the New York Agricultural Experiment Station in 1883 and subsequent years. Fruwirth (1895) apparently did the first work of this kind in Europe. The work of Cannon ('11) on the roots of desert plants, while not presenting in itself any radical departure from work which had preceded it, is important because of the exhaustive way in which the study was made and the completeness with which it was presented; features which were to characterize most of the important work to follow. Perhaps the three most important publications on the subject are the one by Rotmistrov ('10) in Russia and the two by Weaver ('19, '20) in the United States. A paper by von Alten ('09) nicely summarizes the earlier work in addition to presenting some important new material.

## · METHODS

The methods used in this study were the same as those followed by Weaver and his co-workers. The earth from around the roots was carefully and painstakingly removed by means of a small hand pick or similar device, and the roots drawn to scale on coordinate paper in the field. While this method is slower and more tedious than that of root washing, it has so many advantages and gives such superior results that the additional effort is amply justified.

The criteria used in the selection of the five " stations " were, first, an area containing a minimum number of weedy plants, and second, an area in which the root systems of the greatest number of typical prairie plants could be observed with the minimum amount of excavation and labor. In making the drawings, not all of the roots of a single plant were shown, for while it is frequently highly desirable to do so, the large amount of time required for this is often greater than the usefulness of the results warrant. The number of roots drawn for any one plant depended largely upon the judgment of the excavator. It was often necessary to omit many of the excavated roots from the drawings in order to prevent the drawings from becoming so crowded as to be unintelligible.

In general, the drawings show a part of the roots within a vertical section of soil one to two decimeters in thickness. The coordinates in all drawings represent intervals of one decimeter, but much smaller intervals were used in the field. The numbers on these coordinates at each station represent identical lines, so that the true relation of one root system to another root system at the same station can be determined by superimposing lines with corresponding numbers. In the case of figure 2 at the Champaign station, each drawing has its own system of coordinates. The soil surface is indicated either by the zero horizontal line or by a slightly inclined line near the zero line.

## ENVIRONMENT

The five stations selected were located near the towns of Champaign, Rantoul, Kansas, Warrensburg and Peterville (south of Havana), Illinois. The Champaign station, which was the least satisfactory of the five, was located on the Illinois Central Railroad right-of-way about 2 kilometers south of Champaign, near the crest of an Early Wisconsin moraine. The soil (see Hopkins, '18) was a brown silt loam which had an evident line of disturbance at the 45 cm. level. This was probably due to the removal and subsequent replacement of the surface and sub-surface soils when the railroad was double-tracked eight years prior to this investigation. The soil was well drained and well ventilated by means of earthworm burrows and vertical cracks.

A partial investigation of two rosin-weeds (*Silphium*) was made near the bottom of a hill, about 200 meters north of the station. The soil was a black clayey silt loam, and was rather poorly drained. No observations were made on the sod grasses around these two plants.

The Rantoul station was on the Illinois Central Railroad right-of-way 1.67 km. north of Rantoul, and was located in an Early Wisconsin intermorainal area about 1.5 km. south of a morainal ridge. The soil (Hopkins, '18) was a brown silt loam which had had a part of the surface soil removed during the double-tracking. It was quite poorly drained, the water table varying between 190 cm. on July 25, 1932 and 55 cm. on April 23, 1933.

The Kansas station was along the Big Four Railroad right-of-way 3.75 km. west of Kansas, Ill. It was in Early Wisconsin intermorainal glaciation about 2.75 km. north of the Wisconsin terminal (Shelbyville) moraine. The soil is described as Brown Silt Loam on Drift (Smith, '29). It was quite well drained.

The Warrensburg station was on the Illinois Central Railroad right-of-way about 2 km. northwest of Warrensburg, in a Middle Illinoisan intermorainal area, and about 1 km. northwest (outside) of the outer boundary of the Wisconsin terminal (Shelbyville) moraine. The soil (Smith, '29a) was a black clay loam which had a high lime content. The upper 18 cm. of soil had undoubtedly been placed on top of the undisturbed soil below it, probably at the time of the construction of the railroad (about 1875). This station had poor natural drainage.

The last station selected was 0.4 km. north of Peterville, which is 12.5 km. southeast of Havana, Ill. The location was near the crest of a sand dune in a field just east of the Springfield road, on the farm of William Umland. Geologically the site was in a broad terrace on the east side of the Illinois River, about 8 km. southeast of the river and an equal distance northwest of the nearest upland (Middle Illinoisan intermorainal glaciation). The soil (Smith, '24) was a terrace dune sand and consisted of nearly pure coarse yellow sand except at the soil surfaces, both present and past, which contained considerable quantities of a brown loam intermixed with the sand. The present soil had a thickness of about 35 cm. and similar layers were found at depths of 135 cm. and 370 cm. This field, according to Mr. Umland, had been last cultivated about 1890 and had not even been pastured for the last few years prior to this investigation. The pocket gopher (*Geomys bursarius*) was active in the sand in this region, but apparently had not influenced the growth of the roots studied. The water table was found at a depth of 33 dm. on November 7, 1932.

## DESCRIPTION OF ROOT SYSTEMS

The underground parts of the various plants are quite as characteristic of the species as are the tops. Like the tops, each plant is different and has its own individual appearance, yet there are certain characteristics which hold for all members of a given species, and frequently characteristics which are common to all members of the genus, or even of the family. While certain of these characteristics are evident or visible in the drawings, others can better be described by the use of field notes.

· The little bluestem or beard grass, *Andropogon scoparius* Michx.,[1] is shown in figure 7c and was investigated only at the Peterville station. The root system of this plant, as of grasses in general, was of the spreading fibrous type, there being no central, vertically-penetrating root. From 5 to 15 (or more) roots originated from the base of each plant and either ran nearly horizontally just below the soil surface for 2 or 3 dm. before turning downward into the soil, or immediately penetrated obliquely into the soil at various angles to a depth of several (3–8) dm. None, however, was found which penetrated vertically into the soil from the base of the plant. It was very unusual to find, on the other hand, a root which did not penetrate nearly vertically through the soil (in this case, sand) below the 5 or 6 dm. level. The ends of the main roots were found mostly between the 6 and 10 dm. levels, with a maximum depth of 112 cm. recorded.

Numerous branches (second order roots) were produced on these main (first order) roots. These were 2 to 6 cm. in length, and in turn bore third order roots 0.25 to 2 cm. long. Fourth order roots were seldom produced. In general, the branches were longer near the center of the root than near its ends, the second order roots being frequently 5 or 6 cm. long between the 2 and 5 dm. levels, decreasing in length to 2 cm. (or less) at the surface and at the lower ends of the main roots. Exceptions to this, however, were frequent. The diameter of the main roots was 2–3 mm. for most of the length, reaching a maximum of 3.5 mm. and tapering at the lower end to approximately 0.25 mm. The diameter of the second order roots was 1 mm. or less, but roots reaching a diameter of 0.1 mm. were rare. The cortex of the roots was a moderately dark brown, with a slight tendency to become scaly. The stele was a light buff color and moderately strong.

The bulk of the small absorbing roots (designated as the "absorbing region" in the remainder of this paper) were found between the depths of 2 and 90 cm. It will thus be seen that the absorbing region was nearly as great as the extent of the root systems, which is in marked contrast to the conditions found in many other plants.

These plants were fully matured and were shedding their fruit at the time of the investigation. The culms averaged from 7 to 9 dm. in height, reaching a maximum of 1 meter.

Similar notes were kept on all other plants examined, but only the principal features of the subsequent species will be given.

The big bluestem, *Andropogon furcatus* Muhl., is shown in figures 4b, 5b, 6d and 7d. It is one of the most widely distributed of the eastern prairie species. In general appearance the root system resembled that of the little bluestem, but could be distinguished from it by its somewhat larger size, its lighter colored (buff) and more flaky cortex, and its whitish stele. At the Rantoul station, the absorbing region occurred between the 2 and 10 dm.

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[1] All nomenclature in this paper follows "Gray's New Manual of Botany," 7th edition.

levels, while the maximum depth was 118 cm. The second order roots here were unusually long. At the Kansas station, the longest root was lost at a depth of 11 dm., while the absorbing region lay between the 1 and 9 dm. levels. The maximum depths at the Warrensburg and Peterville stations were 177 and 108 cm. respectively, while the corresponding absorbing regions were 5–150 cm. and 5–95 cm. The tops of the plants at the Peterville station were taller (16–22 dm.) and showed more luxuriant growth than those at any other station, while the roots of the plants showed the least depth of penetration of any examined. The radial spread of the plants in the Peterville sand, however, was pronounced, as a lateral extension of 5 dm. was common and a maximum of 85 cm. was found.

The most striking peculiarity found at the Peterville station was that 8 out of the 9 main roots of *A. furcatus* were dead at their lower ends. These had died while the roots were yet young and small, and had subsequently become much thicker without any increase in length. The second order roots near these dead ends, however, were well developed and long (1–4 dm.). They turned downward and produced third order roots which were as large as the "normal" second order roots. It was only upon these large third order roots that fourth order roots occurred. In one case, a second order root had similarly died and had produced a large third order root with correspondingly smaller fourth and fifth order roots. These same characteristics were observed in *A. scoparius* and the rose at this station. In the latter plant eighth order roots were found as a result of continued repetition of this process.

The porcupine grass, *Stipa spartea* Trin. (fig. 3*a*), was observed at the Rantoul station. The thin light colored roots were produced on very short rhizomes and had two types of branches—one very fine and short, the other larger.

The small western drop-seed, *Sporobolus brevifolius* (Nutt.) Scribn. (fig. 7*b*), was found only at the Peterville station, in common with other western species. The longest of the numerous whitish fibrous roots was lost at a depth of 45 cm. so that it seems that the species is rather shallow-rooted.

*Spartina michauxiana* Hitchc., the slough grass (fig. 6*b*), was the dominant species at the Warrensburg station. Its numerous long, tough, scaly rhizomes formed an almost impenetrable mat between the 1 and 8 cm. levels, so that excavation of roots from this layer was very difficult. The roots of this species resembled those of *Andropogon furcatus*, but were lighter in color, less scaly, and more fragile.

The grass shown in figure 6*a* has not been identified with any degree of certainty, so that a description of it here is of no value.

A small early flowering sedge, *Carex varia* Muhl., var. *colorata* Bailey (fig. 4*a*), which was drawn at the Rantoul station, had no unusual peculiarities. The maximum depth found was 83 cm. and the absorbing region lay between the 1 and 8 dm. levels.

An unidentified sedge (*Carex* sp., fig. 4*f*) was characterized by long, horizontal, much branched second order roots. These formed an extensive absorbing region between the 1 and 9 dm. levels. A maximum depth of 103 cm. and a radial spread of 2 dm. was recorded. These plants were found at the Rantoul station.

The roots of the prairie spiderwort, *Tradescantia reflexa* Raf. (figs. 3*e* and 3*f*), were more regularly cylindrical and had a smoother surface than most other roots. The cortex was firm and brown in color, darker near the soil surface but becoming lighter at the tips. A large number of roots (20–40) covered the slightly swollen base of the stem and extended in every direction from vertical to horizontal. The extent of the laterally spreading roots was not determined as these were cut or broken away to allow access to roots of other plants in that vicinity. The greatest radial spread measured was 35 cm., while the greatest depth recorded was 156 cm. Most of the roots, however, did not extend below the 1 meter level, and only one was found below 113 cm. The absorbing region was mainly between 25 cm. and 1 m. Second-order roots were 2–8 cm. long and bore a moderate number of third order roots. Fourth-order roots were rare, and in general not as fine as those of the grasses.

The blue-eyed grass, *Sisyrinchium albidum* Raf. (fig. 5*c*), was small and short-lived, and had a correspondingly small root system. Twenty to forty small and rather fine, brittle, brown, fibrous roots extended 10 to 15 cm. in all directions (below the horizontal) from the base of the plant.

The rose (fig. 8*d*) at the Peterville station had ripened its fruit and shed its leaves when first examined, and so could not be definitely identified. It was probably *Rosa humilis* Marsh. The roots were relatively large and quite irregular. The smaller ones had a dark brown color while the older ones had a characteristic dark red color. The cortex was quite smooth and firm. The death of the principal roots and the subsequent production of main roots of a higher order has already been mentioned. This very irregular growth resulted in an extensive root system which had a radial spread of 40 cm. (or more) and a maximum depth of 80 cm. Certain fragments were found, however, which indicated that the roots might occasionally reach a depth of a meter. The absorbing area was relatively small, but occurred anywhere between the 10 and 80 cm. levels.

The roots of the purple prairie clover, *Petalostemum purpureum* (Vent.) Rydb. (figs. 5*e* and 7*a*) were very crooked and irregular, and had a finely wrinkled cortex and a peculiar buff-yellow color, which made these roots very easy to identify. The short, heavy tap root produced in the upper 20 cm. of soil numerous branches which grew in all directions, even upward. The horizontally spreading roots were lost beyond a length of 20 cm. at the Kansas station and 40 cm. at the Peterville station. A maximum depth of 130 cm. was measured at the Kansas station and 175 cm. at the Peterville station, while the corresponding absorbing regions were 2–120 and 5–95 cm. respectively.

These root systems, in common with those of *Euphorbia corollata,* produced long, prominent, vertically-penetrating second order and higher order roots much as already mentioned in the case of *Andropogon* and *Rosa,* but differed from these plants in that there were no dead ends. These main roots were not located in any specialized area as in the case of the other species, but occurred at almost any point of the system. Except for these " special " vertical roots, only first and second order roots occurred on the plant, but third order roots were observed at the Kansas station, while seventh order roots were found at the Peterville station.

It was at this latter station that a peculiar long *Petalostemum* root was found. It grew 60 cm. deeper than any other root at this station, and was the only root to penetrate through (or even come into contact with) the old soil layer which occurred at the 135–160 cm. level. Only a single root reached and penetrated this layer,—this, strangely enough, passing through the center of an old decayed stem or root which occurred at this point in an upright, vertical position. This root branched several times near its tip. Decayed material like that mentioned above was found in only a few cases in this soil layer.

The flowering spurge, *Euphorbia corollata* L. (fig. 1*g*), had a rather thick tap root with correspondingly coarse branches; a very irregular and crooked growth, in some places perhaps best described by the word "kinky"; an abundance of milky white latex throughout; alternate thickenings and narrowings of the roots, especially of the larger ones; and a rather thin, smooth, reddish-brown cortex on the older parts of the system. This plant especially showed the habit, common to many species, of the coiling of a root upon itself as a result of the growth of the root into a small air cavity in the soil. The drawing also shows at the 30 cm. level a small sub-soil root sprout, a peculiarity observed elsewhere with this species, but not found in any other.

Two small plants of the prickly pear cactus, *Opuntia rafinesquii* Engelm. (fig. 8*e*), at the Peterville station were found to have shallow lateral roots which were traced as much as 30 cm. before becoming lost among the numerous grass roots at this place. No vertical roots were found.

The root system of *Pycnanthemum flexuosum* (Walt.) BSP., the mountain mint (fig. 5*a*), was characterized by numerous long brown obliquely or vertically descending branches of very small diameter. There were borne on the several roots which arose from a single relatively short rhizome. The extensive absorbing region was found between the 20 and 100 cm. levels and a maximum penetration of 117 cm. was observed. It was not uncommon to trace a root 0.2 or 0.1 mm. in diameter for several decimeters before the end was reached.

*Ruellia ciliosa* Pursh. (figs. 1*c*, 1*e* and 4*g*) had numerous fibrous roots produced from the obliquely penetrating rhizomes. A radial spread of 25 cm. was found, and an absorbing region and maximum depth of 10–140 cm. and 149 cm. respectively were measured at the Champaign station. The cor-
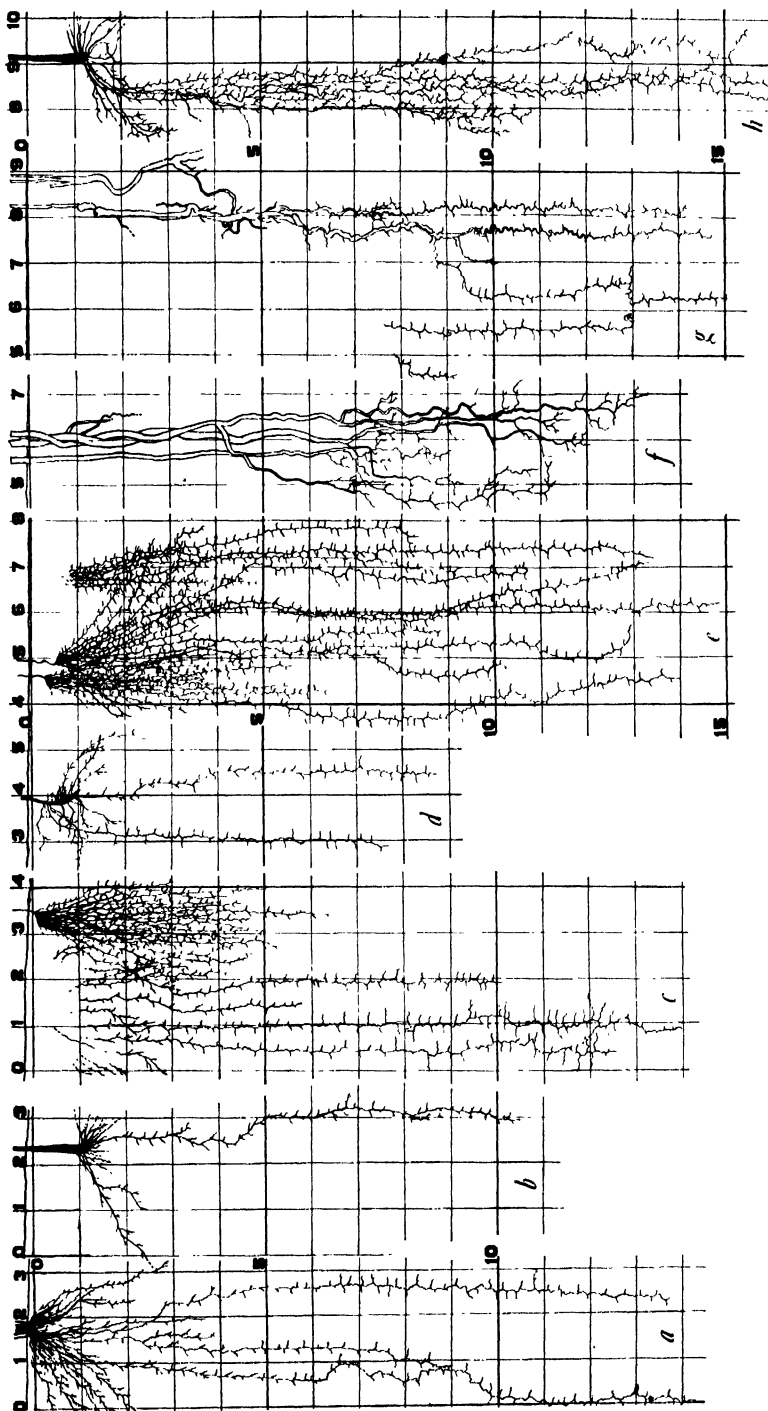
FIG. 1. (Champaign station.) Root systems of *a*, *Lepachys pinnata*; *b*, *Parthenium integrifolium*; *c*, *Ruellia ciliosa*; *d*, *Helianthus scaberrimus*; *e*, *Ruellia ciliosa*; *f*, *Braumeria pallida*; *g*, *Euphorbia corollata*; and *h*, *Parthenium integrifolium*.

responding measurements at the Rantoul station were 20 cm., 10–100 cm., and 110 cm. Second order roots were relatively long, but third order roots were rare. There seemed to be two groups of first order roots, those reaching a level near the maximum depth and those ending at only about half of this depth. The reason for these two groups was not determined. Both the longer and shorter roots had firm, light, slightly swollen tips, which is frequently characteristic of healthy, rapidly growing roots, and which were termed " invader roots " by Waterman ('19). This characteristic was noted in a number of different species.

The blazing star, *Liatris scariosa* Willd. (figs. 5*d* and 8*c*), had a root system which in general resembled that of the *Tradescantia*, but the roots were thinner and whiter. No third order roots were observed. At the Kansas station a maximum depth of 93 cm. was found while the absorbing region extended between the 10–90 cm. levels. The root systems of the plants at the Peterville station were so brittle (due to senility) that satisfactory investigation was impossible.

The roots of a prairie golden-rod, *Solidago rigida* L. (figs. 4*c* and 5*f*), were observed to penetrate obliquely for several (20–50) cm. from the rhizome before penetrating downward. There was nothing else unusual about these roots. They were a medium brown in color and produced second order, and often third order, roots. The maximum depth and absorbing regions were 102 cm. and 30–90 cm. at the Rantoul station, and 140 cm. and 30–140 cm. at the Kansas station.

*Aster oblongifolius* Nutt., var. *rigidulus* Gray (fig. 8*b*) is an attractive blue aster found along the Illinois river which produces numerous brittle fibrous roots from a rather long and slender rhizome. The color of the roots varied from a very light to a dark brown, frequently with a strong reddish tinge. The maximum depth recorded was 70 cm., while the absorbing region seemed to lie between the 2 and 55 cm. levels.

The two plants of *Aster multiflorus* Ait. (figs. 4*d* and 4*e*) which were examined at the Rantoul station were both small, and probably would have had a much larger root system later in the season. The roots resembled those of the *Solidago* but both the rhizomes and the roots were more slender and more brittle than those of the goldenrod. The second order roots were longer and bore longer and more numerous third order roots. The longer root was lost at a depth of 72 cm.

The compass plant, *Silphium laciniatum* L. (fig. 3*b*), had a large fleshy tap root with a characteristic yellowish-brown color and an abundance of clear resinous material which exuded wherever the root was injured. The root was about 5 cm. in diameter near its crown and tapered slowly for the first 20 cm., after which it tapered more rapidly, becoming 1 cm. in diameter at a depth of 60 cm., below which point it again tapered more slowly. The entire root system was crooked and extensive. The maximum depth was 179 cm., while the absorbing region lay between 160 cm. and an undetermined

upper level, probably above 50 cm.   Fourth and fifth order roots were rela-
tively quite long, but were widely spaced as is to be expected in an extensive
(as contrasted with an intensive) root system.

The root system of *Silphium terebinthinaceum* Jacq. (fig. 2*a*) was incom-
pletely examined.   The upper part resembled that of the compass plant, but
was a darker brown and had a more wrinkled cortex.   The deeper portions
of the root system were never excavated.
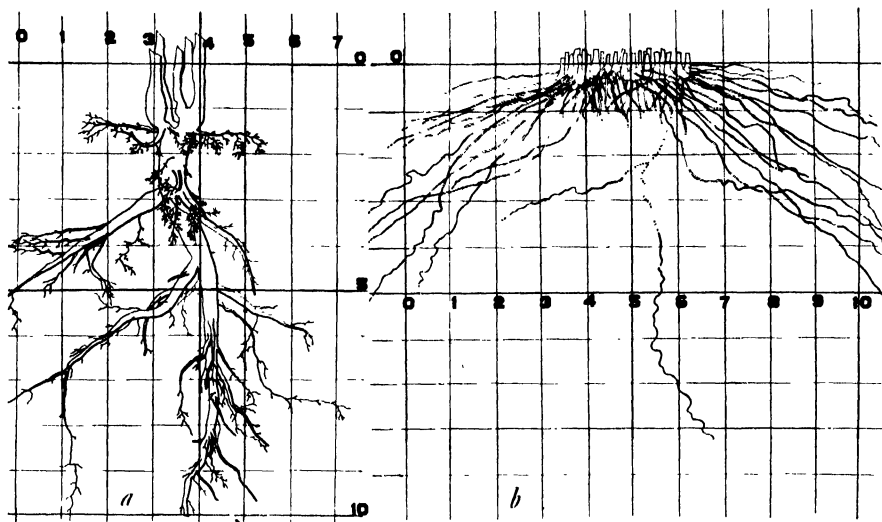


FIG. 2.   (Champaign station.)   Root systems of *a, Silphium terebinthinaceum;*
and *b, S. integrifolium.*

*Silphium integrifolium* Michx. (figs. 2*b*, 3*c* and 3*d*) had a very different
type of root system from the two plants described above.   The plant (or
plants?) formed a mat of many tuberous, slow-growing " rhizomes," an up-
right stalk being produced from each swollen portion of the mat.   The roots,
one or more of which was produced from each of the swollen portions, seemed
never to penetrate vertically downward, but always grew obliquely in the
upper soil layers, although turning downward in the deeper layers.   The one
centrally-penetrating root shown in figure 2*b* penetrated obliquely toward the
observer for several dm. before subsequently turning and passing back under
the mat.   This illustrates a feature which should always be borne in mind
when examining root drawings, that the curvature made by a root is always
as great in the third dimension, i.e., toward or away from the observer, as
in the two dimensions shown.   The deeper portions of the root system did
not differ much from those of *S. laciniatum.*   The roots were well branched
and clearly extensive in nature.   The radial extent, absorbing region, and
maximum depths measured at the Rantoul station were 140, 70–150 and 170
cm. respectively.
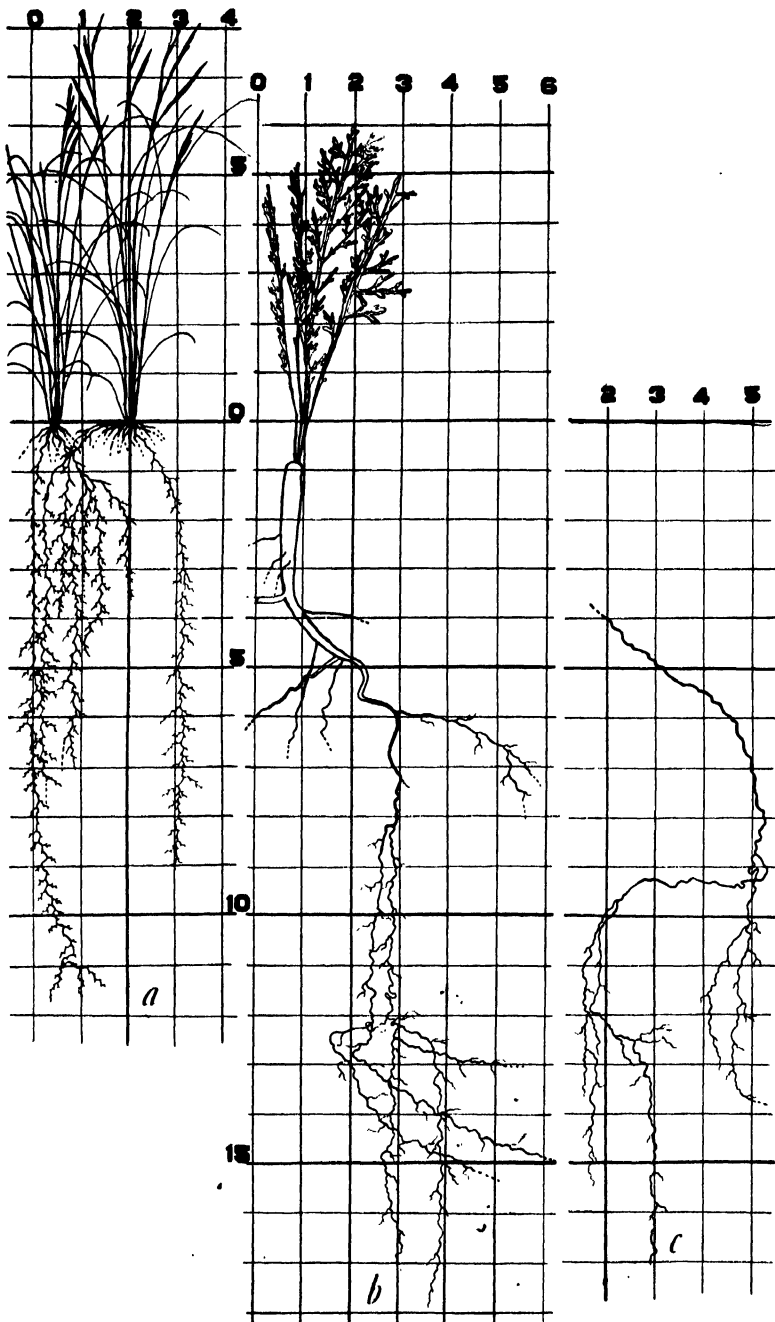
FIG. 3. (Rantoul station.) Root systems of *a, Stipa spartea;*
*b, Silphium laciniatum;* and *c, S. integrifolium.*
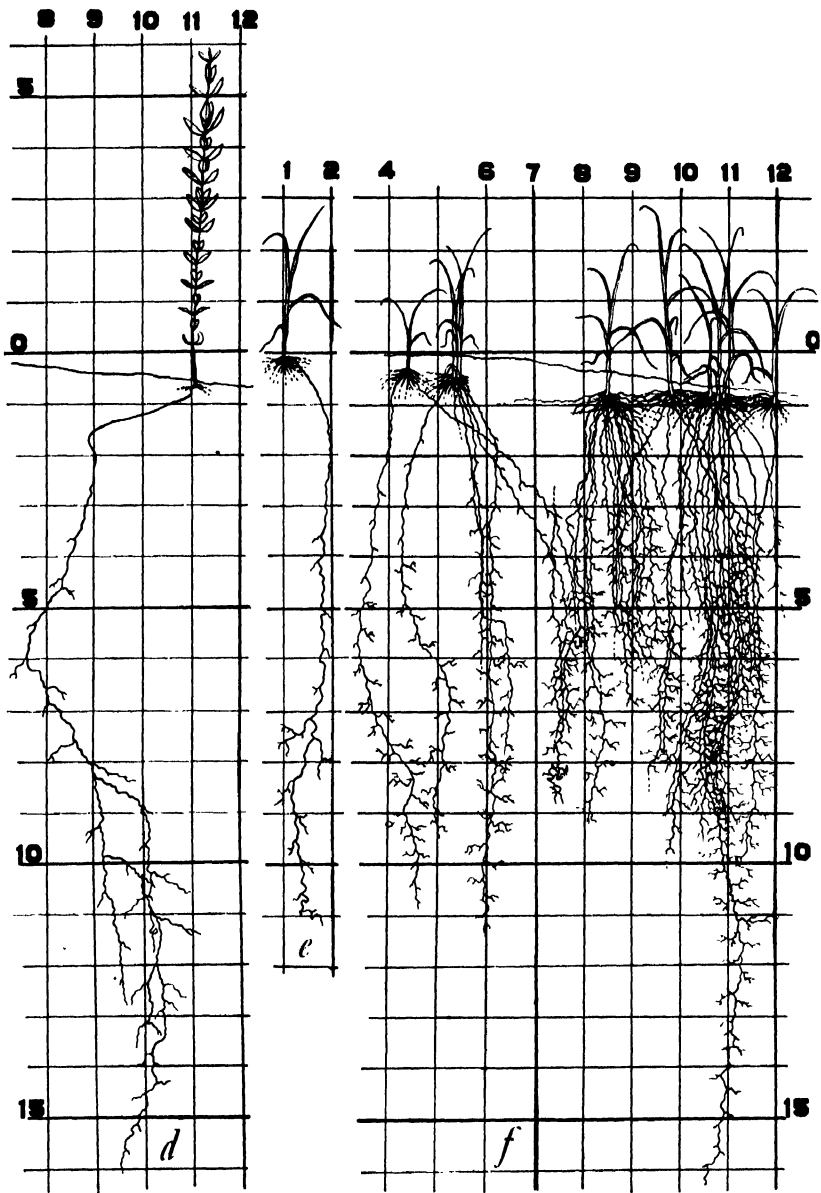
FIG. 3 (continued). Root systems of d, Silphium integrifolium;
e and f, Tradescantia reflexa.
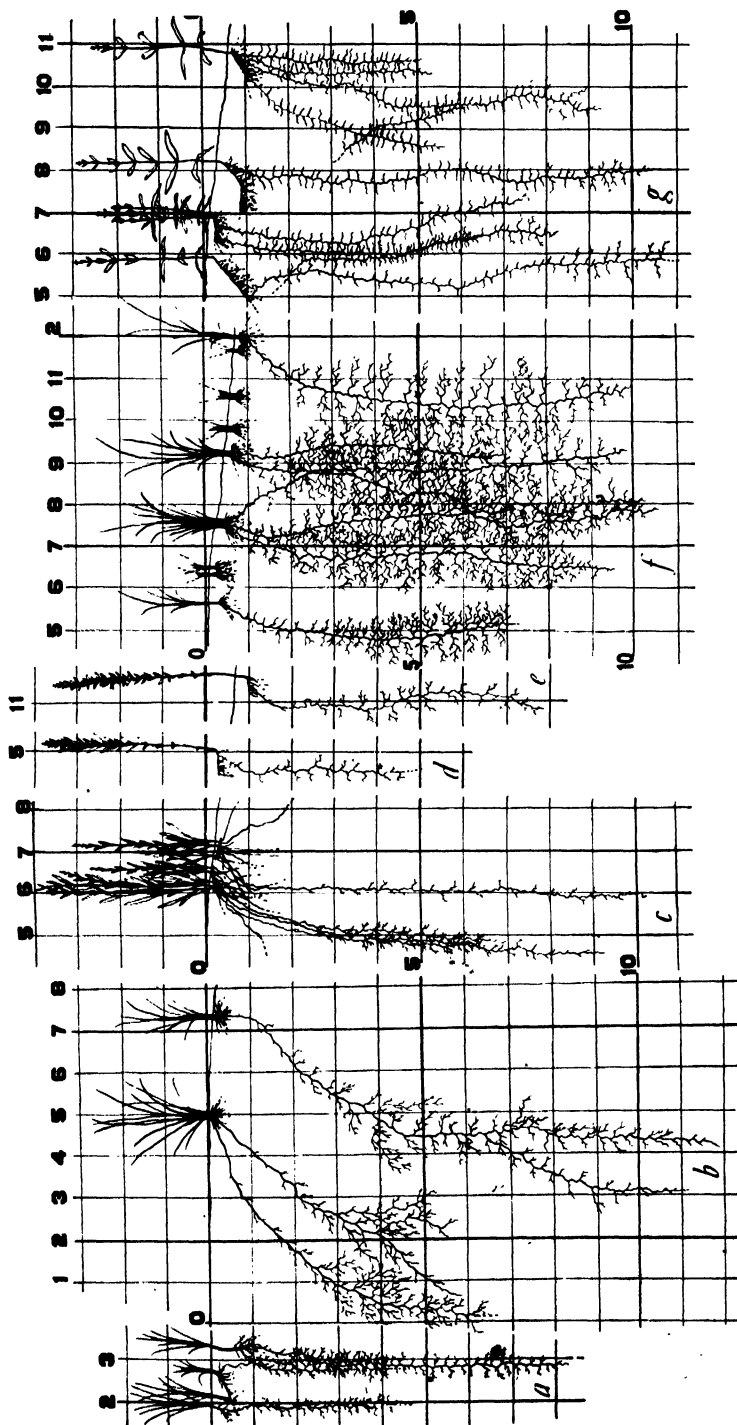
FIG. 4.   (Rantoul station.)    Root systems of a, Carex varia var. colorata; b, Andropogon furcatus; c, Solidago rigida; d and e, Aster multiflorus; f, Carex sp.; and g, Ruellia ciliosa.

Numerous brown fibrous roots were produced from the enlarged base of the *Parthenium integrifolium* L. stem (figs. 1*b* and 1*h*). These did not show any notable characteristics, but the maximum depth, 180 cm., was the greatest depth recorded at any of the five stations. Second order roots were of moderate length, while third order roots were not common.
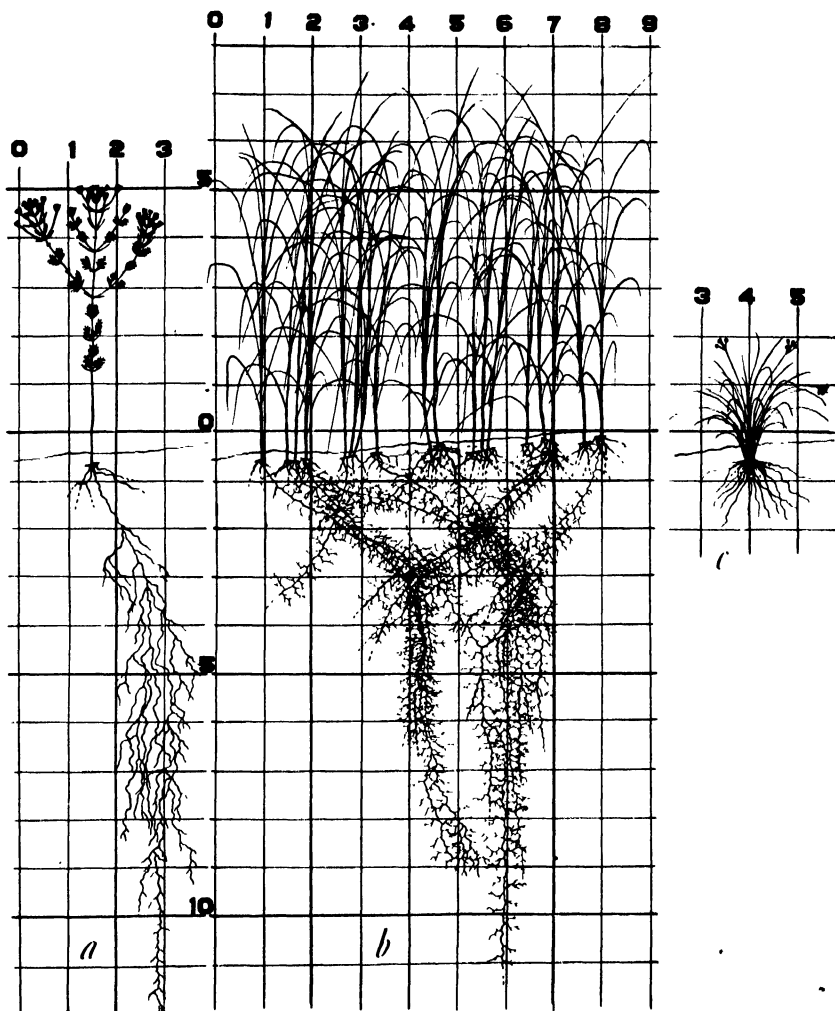


Fig. 5. (Kansas station.) Root systems of *a, Pycnanthemum flexuosum; b, Andropogon furcatus;* and *c, Sisyrinchium albidum.*

The western ragweed, *Ambrosia psilostachya* DC. (fig. 8*a*), had a long thin (1 mm. in diameter) rhizome which was traced for 40 cm. in one case and probably extended twice that distance, judging from the spacing of these plants in the sand. Apparently only one thin tap root is produced per shoot,

this root following a remarkably straight and vertical course.   The sparsely
scattered second order roots were about 1 cm. in length and unbranched.   The
absorbing region extended between the 10 and 100 cm. levels, but the absorb-
ing area seemed remarkably small compared with those of other species.

The purple cone-flower, *Brauneria pallida* (Nutt.) Britton. (fig. 1*f*), had
an extensive root system; twisted and crooked tap roots which were 10–12
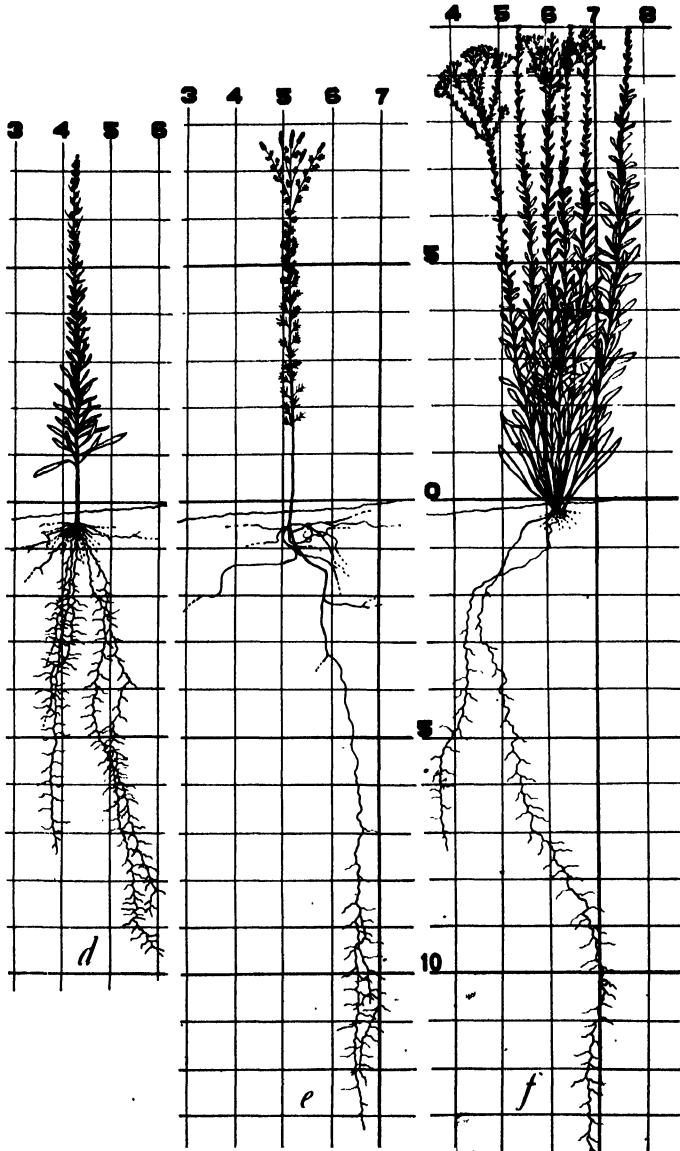


FIG. 5 (*continued*).   Root systems of *d, Liatris scariosa; e, Petalostemum
purpureum;* and *f, Solidago rigida.*

mm. in diameter near the soil surface; a medium brown slightly wrinkled cortex; a deeply placed absorbing region (65 to 120 cm.) ; and unusually large root tips. The maximum depth was 133 cm.

The roots of the prairie cone-flower, *Lepachys pinnata* (Vent.) T. & G. (figs. 1*a* and 6*c*), at the Champaign station grew in nearly all directions from the base of the plant and reached a maximum depth of 145 cm. Some of these fibrous roots were considerably thickened near the base of the plant. Both second and third order roots were frequent in the absorbing region, which was between the 3 and 140 cm. levels. The roots of the plant at the Warrensburg station were so brittle (probably due to senility) that satisfactory investigation was impossible.

The investigations on the root system of *Helianthus scaberrimus* Ell. (fig. 1*d*) were also unsatisfactory, due to the poor location of the plant examined. Numerous rather brittle fibrous roots were produced on the swollen base of the stem, but all were lost at a depth of 88 cm. or less. It is probable that longer roots existed on this plant.

### DISCUSSION AND CONCLUSIONS

One of the most important factors affecting root configuration and penetration is that of oxygen content of the soil. This factor has been studied by Cannon ('24, '25), Howard ('18), Clements ('21), Elliott ('24), and others, and is intimately bound up with that of water table. An equally important factor is that of available moisture. This, perhaps, has been more extensively studied than the effect of oxygen, both by the above authors and by others, notably Jean and Weaver ('24), Weaver ('19, '20) and Shantz ('11).

No measurement of any factors were made when the root systems were investigated, as it was realized that the extent of the roots was not dependent upon the oxygen or water content of the soil at that time, but upon the soil conditions which had been operative at that place during the preceding twelve or more months. It was unfortunately impossible to make extended observations of environmental conditions at these stations. The results obtained must therefore be considered in the light of general climatic conditions and local topography. The latter has already been described, together with the soils, and it is well known that both temperature and rainfall in this region are excellently suited to plant growth. There are occasional dry and occasional wet seasons every few years, and while these naturally have their effect upon plant growth, they seldom if ever result in the death of the plants. The prevalence of fires, pasturage and mowing exert a much greater effect on most of the prairie remnants in this part of the country than do drouth or flooding.

Of the 28 species described, 9 had been studied previously by Weaver and one by Cooper and Stoesz ('31). All of these were prairie and plains plants growing in the drier grasslands west of the Mississippi River, and a comparison of the descriptions of the same species in the two regions reveals the fact
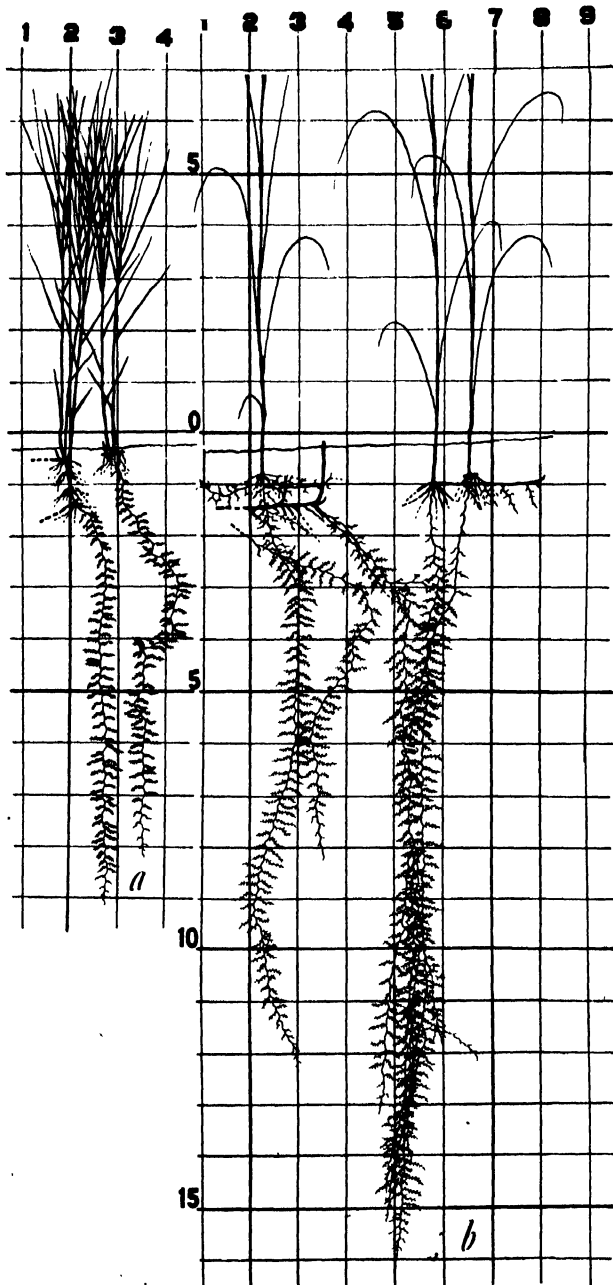
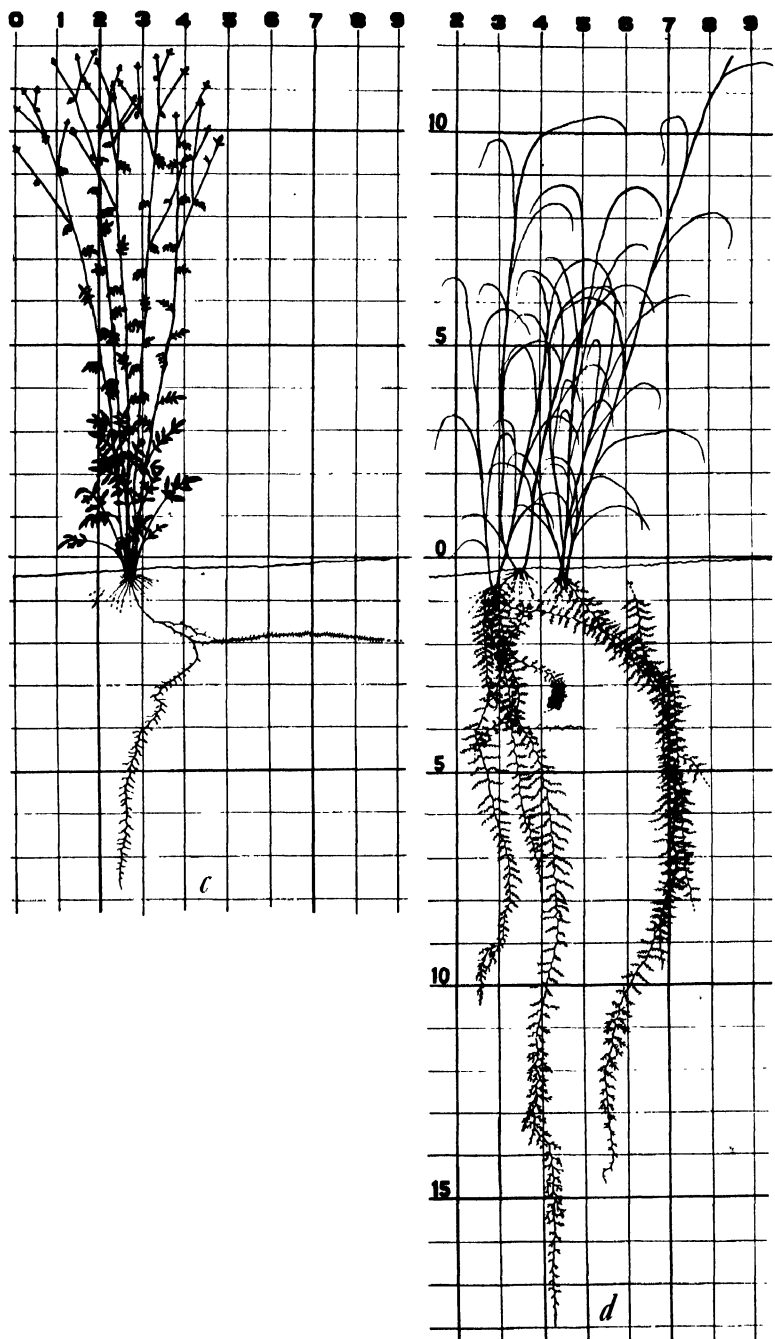FIG. 6. (Warrensburg station.) Root systems of *a;* an unidentified grass; and *b, Spartina michauxiana.*

FIG. 6 (*continued*).  Root systems of *c, Lepachys pinnata;* and *d, Andropogon furcatus.*

that the root systems of the western plants are longer and better developed than those in Illinois.

*Andropogon furcatus,* for example, was found to reach a depth of 274 cm.[2] in the subclimax prairie at Peru, Nebraska, 207 cm. in the true high prairie at Lincoln, Nebraska, 174 cm. in the lowland prairie at Lincoln, 177 cm. at the Warrensburg, Illinois station, greater than 110 cm. at the Kansas, Illinois station, 118 cm. at Rantoul (immature plants?), and 108 cm. in the sand at Peterville (mature plants!). It appears, however, that there was somewhat more branching in the Illinois than in the western plants, though the difference in the number of fine absorbing laterals was not as well marked as the number of larger branches. The extent and total volume of the root systems was undoubtedly greater in the western plants.

Other species show a similar correlation. *Petalostemum purpureum* in the sandhills at Yuma, Nebraska, reached a depth of 256 cm., while 198 cm. was found in the plains near Colorado Springs, Colorado, 175 cm. in the sand at the Peterville station, and 130 cm. in the Kansas, Illinois, prairie. The growth characteristics of these roots at the various localities was remarkably constant.

*Solidago rigida* was found down to a depth of 158 cm. in the prairies of eastern Nebraska, while 141 cm. was found near Kansas, Illinois, and 102 cm. at the Rantoul station.

*Silphium laciniatum* is stated by Weaver to reach a maximum depth of from 274 to 417 cm. in the eastern Nebraska prairies. At the Rantoul station, where it was the deepest root found, a maximum of 178 cm. was reached.

*Brauneria pallida* was found at depths of 130 and 168 cm. in eastern Nebraska, and at a maximum of 133 cm. at the Champaign station. The roots at the latter locality were considerably better branched than those described by Weaver.

The coarse roots of *Spartina michauxiana* were described as penetrating vertically downward distances of 244 to 396 cm., frequently extending into water-logged soil. At the Warrensburg station the maximum penetration was 158 cm., although the soil becomes drained to below this depth during the drier months.

*Andropogon scoparius* is figured by Shantz ('11) as extending to a depth of 152 cm. in sandy soil in eastern Colorado. Weaver found in eastern Nebraska that a maximum depth of 71 cm. was reached in a locality where a sandy and gravelly soil was underlain at 91 cm. with a rocky subsoil of decayed sandstone. At another locality, however, where clay loam was found above a clay subsoil, a maximum depth of 165 cm. was found. He also gave 183 cm. as a maximum at Colorado Springs; 158 cm. near Phillipsburg, Kansas; 107 cm. in the sandhills near Haigler, Nebraska; and 244 cm. in the sandhills at Seneca, Nebraska. The root systems were described as frequently

[2] All of Weaver's measurements were made in feet, but have been converted to the metric system in this paper.
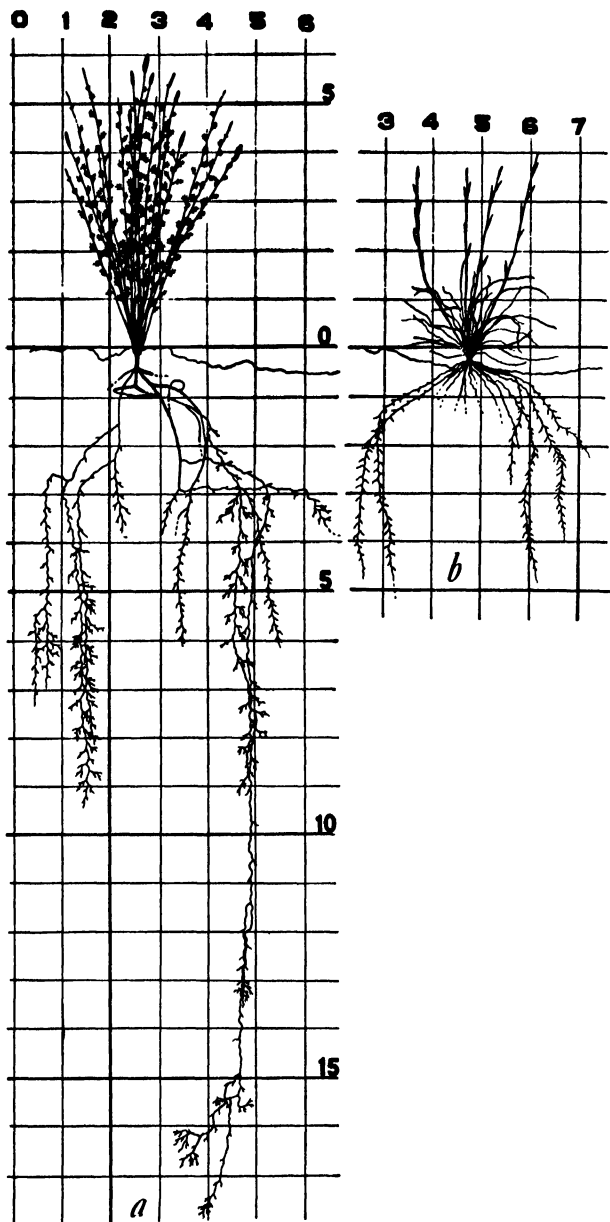
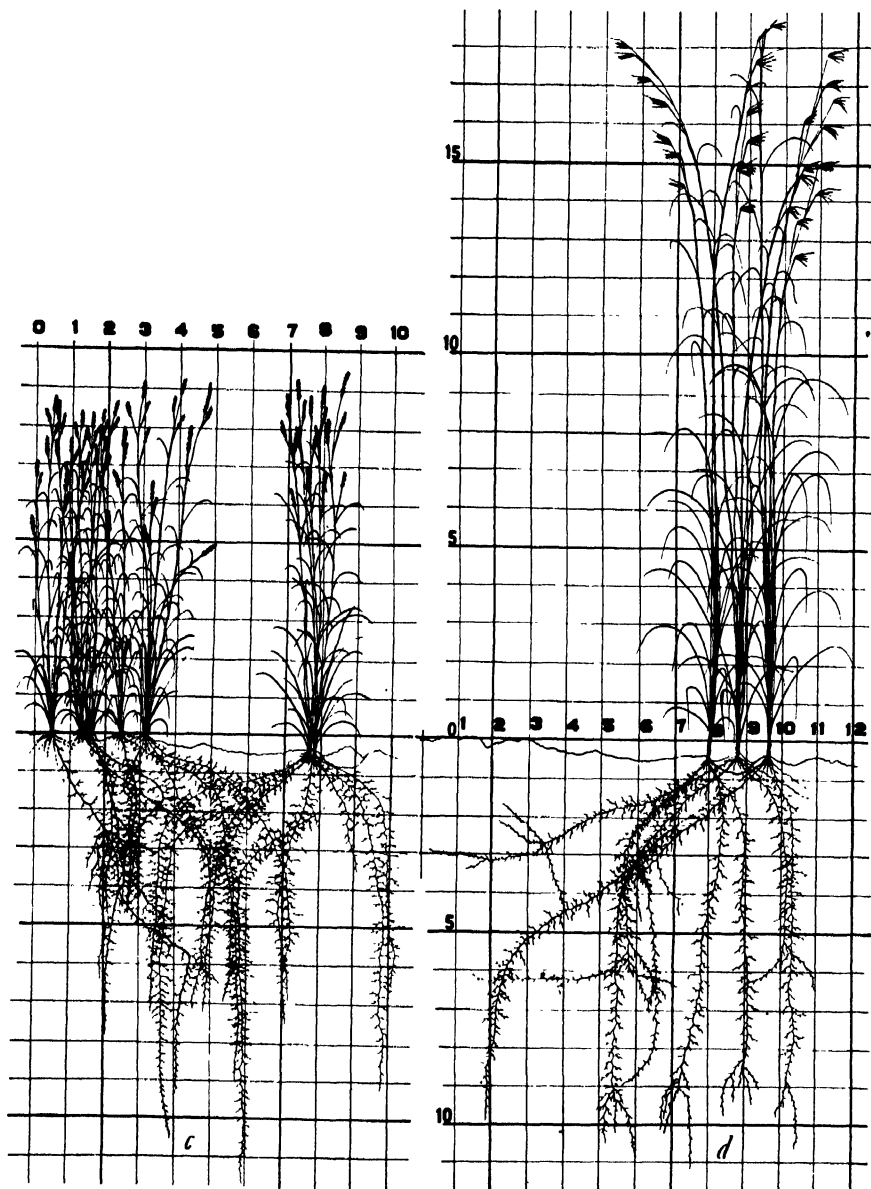FIG. 7. (Peterville station.) Root systems of *a, Petalostemum purpureum;* and *b, Sporobolus brevifolius.*

FIG. 7 (continued). Root systems of c, *Andropogon scoparius;* and d, *A. furcatus.*

being quite wide spreading, growing radially near the surface 91 to 122 cm. This lateral spread was apparently more pronounced in those places where vertical penetration was relatively small. In the sand at Peterville, Illinois, a maximum depth of 114 cm. was reached, with a radial spread of not more than 45 cm. The wide spreading character of these roots resembled that described by Weaver.

Only in *Stipa spartea* was the root system larger in Illinois than in the western prairies. Weaver described these roots as being meager as compared with those of other prairie grasses, and found the greatest penetration to be 53 to 64 cm.[3] At the Rantoul station, however, the root system, while composed of relatively fine roots, was as well developed as that of any of the other plants at the station. A maximum depth of 117 cm. was measured, the absorbing region extending between the 10 and 90 cm. levels, with a radial spread of 20 cm.

Only two of the plants investigated in the Illinois prairies were genetically shallow-rooted, *Opuntia rafinesquii* and *Sisyrinchium albidum*. The root system of the *Opuntia* is in agreement with Cannon's statement that the roots of most cacti are of a specialized type, and are inflexibly shallow. Two other plants in the Peterville sand, *Sporobolus brevifolius* and *Aster oblongifolius*, var. *rigidulus*, also had relatively small root systems, but it is not known whether this is a genetic character of the species, or is due to the character of the habitat.

The root systems of the other 14 species would be classed as neither meager nor shallow. Some were among the best developed roots found, while others had peculiarities which warrant further investigation.

It cannot be purely a matter of coincidence that the roots examined were regularly shorter than those investigated in the western grasslands, and that no roots were found deeper than 180 cm. It seems that there are only three factors operating at the first four stations which might prove to be limiting in their effect upon the development of root systems. They are abundance of soil moisture, water table, and lack of oxygen, all of which are a result of either an abundant rainfall (35–40 inches, 60% of which occurs during the growing season) or relatively poor drainage, or both. As noted by Weaver, Cannon, and others, a soil in which the water content is slightly below the optimal amount for the development of the shoot, results in the most extensive growth of roots.

At the Peterville station, however, another factor enters, that of mineral nutrients. It is known that this soil is extremely low in nitrogen, with potassium as a secondary limiting element (Hopkins, '12, pp. 122–124. See also Waterman, '19). This station, therefore, is in direct contrast with the Nebraska sandhills, which contain an abundance of the necessary mineral nutrients for plant growth, but lack only water (Weaver, '20, page 97). The

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[3] A recent communication from Dr. Weaver states that in 1934 several roots of this species were found at a maximum depth of 150 cm. in eastern Nebraskan prairie.
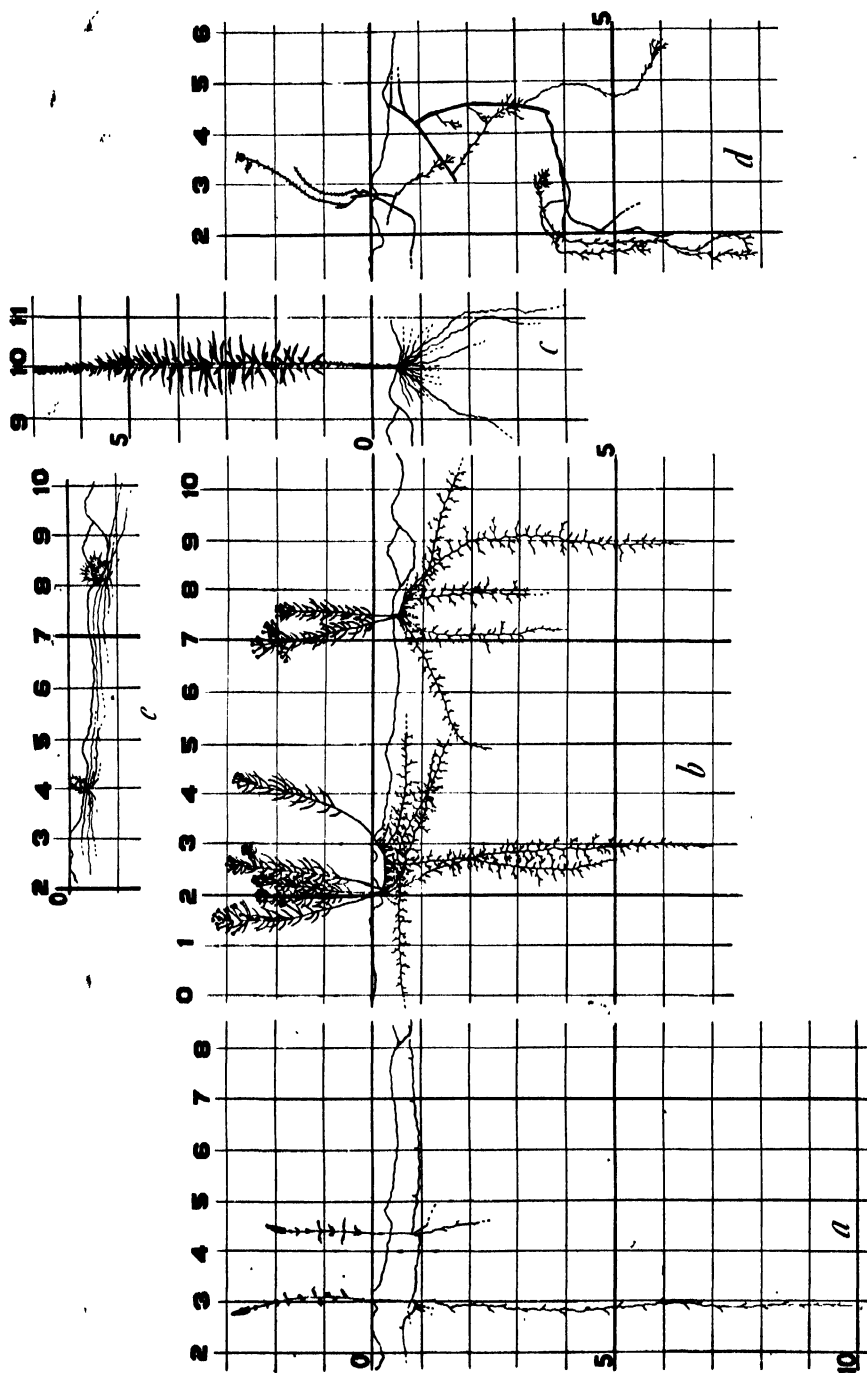
Fig. 8. (Peterville station.) Root systems of a, *Ambrosia psilostachya*; b, *Aster oblongifolius* var. *rigidulus*; c, *Liatris scariosa*; d, *Rosa* sp; and e, *Opuntia rafinesquii*.

Peterville soils always retain sufficient moisture for plant growth, only the top few cm. drying out during rainless periods. The fact that the one *Petaloste-mum* root was able to penetrate so much deeper than any of the other roots at this station is in accord with the observation that nitrogen is the limiting factor for root growth at this station, since this plant is a legume and is independent of a supply of combined nitrogen.

While no measurements of weight or volume of roots and shoots were made during this investigation, it was readily noted that while the root systems were plainly less well developed in Illinois than in the western prairies, the growth of shoots is always as great, and often greater, in the former than in the latter regions, thus giving a smaller root-shoot ratio in the Illinois plants investigated than that found by Weaver. This conclusion agrees with the observation that a greater supply of soil moisture (near the optimum for shoot development) results in a less extensive root development, but does not agree with Jean and Weaver's conclusions concerning crop plants ('24, page 60) that yield varies directly with root development.

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# FLUCTUATIONS IN BIOTIC COMMUNITIES

## I.  PRAIRIE–FOREST ECOTONE OF CENTRAL ILLINOIS

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The ecotone between deciduous forest and prairie is a tension zone which, by virtue of biotic forces, growth forms, and mores characters, results in a very unstable condition with dynamic annual, seasonal, and diurnal fluctuations in the biota.  Although of composite character, the emergent result is, in some degree, a totally new community characterized by a different biota, or a somewhat changed or modified mores on the part of the constituent biota usually considered characteristic of either or both of the adjoining biomes (Bird, '30, p. 362).  The entire tension area may be termed ecotone of the first order to distinguish it from the ecotone of the second order which is composed of forest edge thickets of individual forested plots in the larger tension zone.  Plant studies in areas of this type have been made in various areas by Weaver and Himmel ('17), Pool, Weaver, and Jean ('18), Vestal ('18), Hanson ('22), and Clements and Weaver ('24).  Biotic study of such areas has remained untouched.

As has been pointed out by Shelford ('13) and Weese ('24) this area has its own fauna which ranges into the adjacent grassland and forest communities; certain plants likewise have an overlapping zone of distribution in the second order ecotone.  There is an environmental gradient within which, for the animals at least, exist a variety of micro-climates.  Hence the entire biota is essentially a composite of forms of adjoining communities, but also includes indigeneous forms which often form an important part of the perennial nucleus.

The area studied was in the ecotone parkland and savannah area of Illinois.  Patches of woods and outlying thickets in the area originally occupied by the river forest of the Salt Fork of the Vermillion river in the vicinity of Urbana, Champaign County, Illinois, were selected as being representative relics of former wide spread communities.  The woodlands selected are. known locally as the Brownfield Woods (sec. 1, T 19 N, R 9 E) and the University Woods (sec. 34, T 20 N, R 9 E) and previously have been studied by McDougall ('22, '25, and '28), Weese ('24), Telford ('26), Blake ('27 and '31), and Smith-Davidson ('28, '30, and '32).  Prairie communities nearby have been studied by Shackleford ('29) and Rice ('31).  The forest border of thicket and brush in its original undisturbed condition occupied a width of approximately .004 miles.  In northern and central Illinois this probably totaled one per cent of the total area.

The original larger animals have all been removed from the tracts studied with the settlement of the adjoining areas (Wood, '10) ; the smaller forms up to and including the cottontail rabbit, raccoon, and perhaps opossum are still present.

## METHODS AND CRITERIA

The method of sampling was essentially that of Weese ('24, p. 10), fifty sweeps of the insect net being used as a sample of the invertebrate population of the vegetation, while the standard unit for the ground samples was the square meter.   Notes concerning the numbers of birds and mammals were obtained by cruising through the forest edge over a route about a mile long making note of all presences and evidences in a strip twenty feet wide.   Collections and observations were made from February 1932 to June 1933.   •

The terms used in designating degrees of abundance and influence are those of Smith ('28, p. 484). *Dominant* and *subdominant* are used for plants, *predominant* and *major influent* for vertebrates, and *influent* and *subinfluent* for invertebrates.   The category based on being " active " or " present " throughout the entire year (criteria of Smith) is not altogether valid because life stages may be present which are not taken in the sampling techniques used.   In this study the actual statistical samplings were supplemented at all times by cruising and observation.   The terms *predominant* (permanent resident) and *influent* indicate, therefore, that no marked lateral migration takes place on the part of the species, with the result that no conspicuous part of the life history is spent outside of the community in question.   A species failing to occur in collections or to be evidenced by cruisings in adjoining communities was considered as being in a non-conspicuous stage in the habitat where the adults were last taken.   Certain forms designated as *predominants* may not as individuals be present throughout all periods of the year : species such as many birds and the bison in certain portions of its range under undisturbed conditions may, in spite of the migration of all individuals, occupy permanently the area between the southern summer and northern winter limits of the total specific range.   Hence some members of the species may be present in the area at all aspects and the term *predominant* is used here with this concept in mind.

## THE FOREST EDGE AS AN ECOTONE COMMUNITY

*Perennial nucleus: Cercis-Cornus-Cardinalis-Ceratomegilla Associes*

The perennial nucleus of this community is ćomposed of the *dominants,* *predominants,* and *influents.*   The community aspect is one approaching that of forest reproduction, but the large trees are lacking.   The thicket·type of habitat provides a favored place for many birds the year around and formerly provided protection for the large browsing and grazing predominants from the contrasting non-thicketed forest interior and⚘prairie.   Wood ('10) lists 19 species of predominant mammals which°once made their permanent resi-

TABLE I. *Biotic composition of the Forest Edge community throughout the year. Forms in brackets now extinct. Forms marked by asterisk (\*) not native in area.*

## FOREST-EDGE BIOTIC COMMUNITY
### Champaign County, Illinois

dence or spent a greater portion of their time throughout the year in the forest edge. In general, the predatory-niche portion of the animal population was least changed in aspection, probably because the movements of these individuals are only secondarily caused by the distribution of the foliage.

## ASPECTION: SEASONAL FLUCTUATION

### Prevernal Aspect: Aesculus-Claytonia-Junco-Corythuca Socies

The prevernal period began in the forest edge with the arrival of the first spring birds (Feb. 15, 1933) and lasted until May 1. This period was characterized by the growing up and maturing (blossoming: anthesis) of ground cover vegetation, and the flowering of certain shrubs and trees (*Cercis, Cornus, Aesculus, Benzoin, and Ulmus*). Earliest of the plant evidences was the appearance of *Peziza* cups and the budding of the buckeye and elm. By April 2 the aspection had greatly progressed with the mean weekly temperature rising to 46.5° F. as compared with 33° for the preceding week. On the later date many Diptera were flying and the first ground blossoms appeared. The migrations of many birds took place during this and the following aspect and since the majority were thicket-inhabiting birds, the forest edge was their stopping place while passing through the area. The bulk of the invertebrate phyllophagous population distributed itself in strata having leaves, thus making an apparent upward migration from the duff stratum starting about April 2 and culminating in the tree layer May 1, the termination of the prevernal aspect. Certain of the species ceased their migration in the strata to which they were physiologically best adapted and in which they remained (save for diel migrations) throughout the summer. During this period the entire active biota of the forest interior and the forest edge was markedly similar.[1] A greater bird population was, however, found to be present in the forest edge community.

### Vernal aspect: Aesculus-Arisaema-Warbler spp.-Blissus Socies

Migration outward from the forest edge and interior on the part of the invertebrate migrants (chiefly insects) and the moving of a large part of the total bird population of the entire area to outlying thickets and hedges characterized the vernal period; this was coupled with the replacement of the ground cover vegetation by the foliage of the dominant trees and bushes of the thickets. Insects hibernating in the forest interior, were, in general, to some degree associated with either the forest edge or interior during the later seasons although this was not universally true. Migrant birds not present during the winter occupied the outlying thickets separated from the woods proper while the hiemal resident migrated to other portions of their geographic range. Thus while the general bird population migrated to the outlying forest edges, but little evidence was found showing that this was individually characteristic of any species.

[1] For data concerning the adjacent communities referred to here and elsewhere see Carpenter ('34a).

*Aestival aspect: Aesculus-Ostrya-Ceresa-Ormensis Socies*
*Serotinal aspect: Aesculus-Vernonia-Dicyphus-Apion Socies*
{Open season birds}

The aestival and serotinal seasons are defineable only by invertebrates. The birds apparently show no recognition of these periods in their habitat selection although second brood breeding habits might prove enlightening here. These two periods are both characterized by the breeding and developmental stages of many species which hibernate either in the forest interior or margins. Few species are present in the forest edge at this time which spend the Hiemal period elsewhere than in areas controlled by forest. The serotinal period was further characterized by a large number of Compositae.

*Autumnal aspect: Vernonia-Warbler spp.-Diabrotica-Lygus Socies*

The Autumnal socies was characterized by the inward migration of many insects which had spent the summer months in the meadowlands. These moved into the forest edge at the strata of their summer habitat, and during the latter portion of the period the migratory population moved downward from breeding strata to those of hibernations, some time being spent in each stratum traversed en route. This phenomenon was first observed by Weese ('24) and has been confirmed since by other workers.

*Hiemal aspects:* $\begin{cases} Nuthatch\text{-}Kinglei\text{-}Xysticus\ Hiemal\ Presocies \\ Ceratomegilla\text{-}Blissus\text{-}Lygus\ Hibernal\ Socies \end{cases}$

The hiemal aspect is characterized by two well defined types of reaction: (1) those in which individuals undergo hibernation and assume a condition of dormancy, and (2) those in which the forms are active throughout the winter and reduce their activity to a minimum only on the coldest days. The former form a Hibernal socies composed of all vegetation, and the majority of the invertebrates, excepting only certain spiders which are active on the warmer days and evidence a low threshold point in regard to activity. The winter birds and mammals however carry on for the most part, but since their activity alone characterizes the period, the term presocies is permissable here. The Hiemal period began about December 1, 1932 with the cessation of movement by the greater part of the insects hibernating in the duff stratum. Further activity consisted of slight shifting about in the layer of hibernation by some species and the roaming of a few hardy spiders over the vegetation and old stalks presumably in search of frozen aphids and plant bugs.

### FACIATION: THE EFFECT OF EXPOSURE ON POPULATIONS

The effect of exposure of the forest edge with reference to wind, sunlight, etc., has been much accentuated by the creation of isolated groves by man and the removal of the forest brush to the boundaries of woodlots in

many cases. This constitutes a facies difference which affects only certain of the biota as will be noted below. The insect population appeared, in general, to be but little affected by the direction of exposure in the selection of hibernation spots. Prevernal activity was retarded in the northern exposures however. The selection of habitat by birds in this regard is particularly evident in the hiemal period; protection from the prevailing cold west and southwest winds forced the birds to select the " lee " side of the woods in both tracts observed (Carpenter, '35). The differential effects of exposure on vegetation was noticed in that on the west side of both woods the grasses of the surrounding territory had invaded the forest edge floor to a greater extent than on the other sides. Under primitive conditions prairie fires also had a profound effect on the windward forest margins.

## Diurnation: Diel Fluctuation

Fluctuation in community constituency throughout the 24 hours of a day is known as *Diurnation;* events which occur within the confines of a 24 hour day are known as *Diel* phenomena. Periods of the day are recognizable by characteristic activity on the part of the biota much in the same way as are the seasonal periods of a year; these diel periods are termed *phases* (Carpenter, '34b). Although the differential effects of time of day have long been appreciated by physiologists, and the collecting methods of economic entomologists and taxonomists in general have taken this into account, serious study from a community viewpoint has been avoided. Some work has been done by the autecologists on strictly nocturnal animals and their rhythms of activity; a review of this work has been presented by Crawford ('34). The effect on biotic inter-relationships has received but little attention.

Sanders (data, '14, published, '22) in the Chicago area, Gudoshikova ('27) in the vicinity of Perm, U. S. S. R., and Davidson and Shackleford ('29) in Oklahoma all found marked fluctuations in collections made at different diel periods although only the latter workers made collections throughout the entire 24 hours. In all cases the differences between the phases were significant and warrant further study.

Diel collections were made during the Prevernal and Autumnal period in the forest edge and areas adjacent (forest interior and adjoining grasspatch) and fluctuations occurred as shown in chart 1. Greatest fluctuation appeared in areas having the greatest herb population; in the autumn this was the forest edge; in the prevernal, the forest interior. Autumnal vertical migration was most noticeable with *Notoxus monodon, Harpalus* spp,, and *Empoasca viridescens.* There were horizontal migrations from the woods into the open during the day by *Lygus pratensis, Diabrotica vittata, Phalacrus politus,* and reverse movements by *Euschistus* spp. and *Dicyphus gracilentus.* Prevernal migrations were also chiefly lateral, with migrations to the forest edge from the interior by *Epitrix brevis* and *Sympychnus lineatus* during the afternoon. The same vertical migrations occurred here in reverse direction as in the autumn. In the autumnal study the vesperal and early nocturnal periods appeared the

same while in the latter study they were distinct; however after 10 P.M. and until 4 P.M. many Muscidae were taken by a light trap which had not attracted any of that group before that time.   Other differences in the period of nocturnal activity may have been the result of a rain storm which lasted
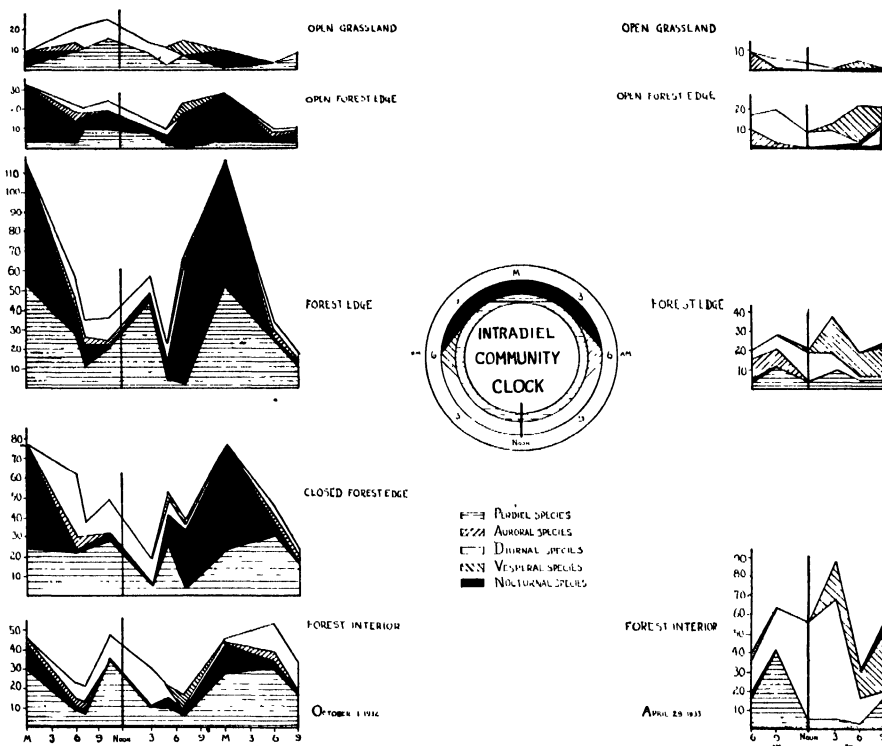


CHART I.  Fluctuations of total populations during the several intradiel phases of the Autumnal and Prevernal Socies.  The graphs are of the "cumulative" or "analysis" type, the top plotting indicating the trend of the total population at any given time.

from 11 P.M. till 3:30 A.M.   A tabular expression of the phases is given in Table II.[2]

[2] The terms used to designate the portions of the day are those introduced by the author (Carpenter, '34b) :

Intradiel: Pertaining to phenomena taking place within the confines of a single 24-hour day.

Phase: Intradiel subcommunities; equivalent to " seasonal society " in aspection.

Auroral: Pertaining to the dawn or morning crepuscular period; from the first appearances and influences of daylight to the effect of the heat of the day (about mid-morning).

Diurnal: Pertaining to the portion of the day which is free from the nocturnal and crepuscular influences (i.e., chiefly decreased light and increased humidity).

Vesperal: Pertaining to the evening crepuscular period; the complement of auroral.

Diel: Pertaining to the day in the sense of the 24 hours.

Diurnation: The phenomenon of diel fluctuation in community composition, i.e., within a single day (equivalent to aspection: the fluctuations within a single year).

TABLE II. *Intradiel phases of two seasonal socies in a forest edge*

| Phase | Autumnal socies | Prevernal socies |
|---|---|---|
| DIURNAL | *Diabrotica vittata*<br>*Empoasca viridescens*<br>*Ceratomegilla fuscilabris* | *Sympycnus lineatus*<br>*Empoasca viridescens*<br>*Wala palmarum* |
| VESPERAL | *Harpalus erythropus*<br>*Notoxus monodon* | *Phalacrus politus*<br>*Glyptina spuria*<br>*Epitrix brevis*<br>*Notoxus monodon* |
| NOCTURNAL | *Epitrix brevis*<br>*Lygus pratensis* | MUSCIDAE<br>*Fontaria* sp. |
| AURORAL | *Wala palmarum*<br>*Phalacrus politus* | *Sympycnus lineatus*<br>*Ceratomegilla fuscilabris* |

## SUMMARY

From the study it was apparent that communities of ecotone areas do not exist as isolated entities although each has its peculiar dominants. Certain predominants formerly ranged, and many major influents still range throughout the environmental gradient both diurnally and seasonally, thus binding it into a unit complex characteristic of the ecotone. As in the case in all complexes or combinations, the emergent is not wholly the sum of its component phenomena: migrations between communities of the complex are not possible with isolated communities as such.

The movement into hibernation quarters constitutes one of the most important features of the Illinois complex of communities studied. This, together with the diel migrations indicated a marked tension condition resulting in strikingly different micro-climatic conditions in different parts of the day and year. This tension may be due to some extent to the disturbed surrounding areas which were but poorly buffered from the areas studied; however, tension zones are present under both natural and cultural conditions and the net difference is not great. Tension was expressed by both horizontal and vertical migration which was greater in the forest edge than in the other communities of the complex. These migrations resulted in periodic changes in the animal constituency of the community forming phases of the seasonal socies which may be characterized by several species.

## ACKNOWLEDGMENTS

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# CATASTROPHIES AND PURE STANDS OF SOUTHERN SHORTLEAF PINE [1]

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In the spring and summer of 1934 age determinations were made of a considerable number of southern short leaf pine trees, *Pinus echinata* Miller, in Howard County, southwestern Arkansas. In the stony foothills of the Ouachita Mountains three areas of locally-designated virgin pine were studied and in each there existed a certain uniformity of age of trees that contrasted with true virgin stands, in which a wide and even distribution of age classes is usually found. . The following is a table showing the age distribution of all trees on designated numbers of one-fourth acre plots.

Table I shows that 68.57 per cent of the stand in area *A* became established in the nine year period between 1858 and 1867; similarly in area *B*, 63.16 per cent of the stand in the ten year period between 1812 and 1822, and in area *C* 85 per cent in the fifteen years from 1772 to 1787. The percentage of stand which came in before these periods is area *A*, 8.57; area *B*, 8.27; and area *C*, 5.0. Trees coming in after the periods made up the following percentage: area *A*, 22.86; area *B*, 28.57; and area *C*, 10.0. In all three instances the closing of the period of intensive reoccupation was not as sharply marked as the beginning.

It is known among southern foresters and lumbermen that purity of composition and uniformity of age in pine forests are the usual indicators of an " old field " stand, or the consequence of some catastrophe that wholly annihilated the previous plant cover. This is to say, a denuded area which is edaphically favorable, and which has seed-trees near, is soon seeded to pine and within the span of a few years a plant cover develops which for the most part resists further invasion of both hardwoods and members of its own species. From the foregoing data the natural inference is that some catastrophe destroyed practically all the forest in areas designated *A*, *B*, and *C* near the years 1857, 1811, and 1770 respectively. As enumerated above, certain seedlings and some older trees escaped. There followed a certain period in which the areas were intensively reoccupied by a growth of pine, followed in turn by a longer period during which a greatly diminished number of trees came in at irregular intervals. Hence the present stand is composed of three hypothetical classes, (1) older trees of the original stand and (2) seedlings that survived, and (3) reproduction following the disaster.

Although this section was settled in the early part of the last century, the extensiveness of two of the areas and the unsuitability of all for farming purposes seem to preclude the possibility of their having been cleared for this

TABLE I. *Age of trees in stands of Pinus echinata in Howard County, Arkansas*

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | **Area A. 3 plots** | | | | |
| Age | Year of germination | No. of trees | Age | Year of germination | No. of trees | Age | Year of germination | No. of trees |
| 82 | 1852 | 2 | 72 | 1862 | 7 | 63 | 1871 | 3 |
| 80 | 1854 | 2 | 71 | 1863 | 2 | 62 | 1872 | 1 |
| 78 | 1856 | 1 | 70 | 1864 | 8 | 58 | 1876 | 4 |
| 77 | 1857 | 1 | 69 | 1865 | 6 | 57 | 1877 | 1 |
| | | ———¹ | 68 | 1866 | 2 | 55 | 1879 | 1 |
| 76 | 1858 | 6 | 67 | 1867 | 3 | 54 | 1880 | 2 |
| 75 | 1859 | 3 | | | ———² | 41 | 1893 | 1 |
| 74 | 1860 | 7 | 66 | 1868 | 1 | | | |
| 73 | 1861 | 4 | 64 | 1870 | 2 | | | |

Total number of trees—70.      Mean age—69.5 years.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | **Area B. 7 plots** | | | | |
| 213 | 1721 | 1 | 119 | 1815 | 6 | 107 | 1827 | 2 |
| 174 | 1760 | 1 | 118 | 1816 | 12 | 106 | 1828 | 4 |
| 173 | 1761 | 1 | 117 | 1817 | 2 | 105 | 1829 | 4 |
| 152 | 1782 | 2 | 116 | 1818 | 13 | 104 | 1830 | 1 |
| 151 | 1783 | 1 | 115 | 1819 | 14 | 102 | 1832 | 1 |
| 149 | 1785 | 1 | 114 | 1820 | 6 | 101 | 1833 | 1 |
| 127 | 1807 | 1 | 113 | 1821 | 2 | 100 | 1834 | 2 |
| 125 | 1809 | 1 | 112 | 1822 | 6 | 99 | 1835 | 2 |
| 124 | 1810 | 2 | | | ———² | 97 | 1837 | 1 |
| | | ———¹ | 111 | 1823 | 2 | 95 | 1839 | 1 |
| 122 | 1812 | 8 | 110 | 1824 | 5 | 86 | 1848 | 1 |
| 121 | 1813 | 5 | 109 | 1825 | 5 | 76 | 1858 | 1 |
| 120 | 1814 | 10 | 108 | 1826 | 5 | | | |

Total number of trees—132.      Mean age—117.3 years.

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | **Area C. 1 plot** | | | | |
| 164 | 1770 | 1 | 157 | 1777 | 1 | 149 | 1785 | 2 |
| | | ———¹ | 156 | 1778 | 2 | 148 | 1786 | 1 |
| 162 | 1772 | 2 | 155 | 1779 | 1 | 147 | 1787 | 2 |
| 161 | 1773 | 1 | 154 | 1780 | 1 | | | ———² |
| 160 | 1774 | 1 | 153 | 1781 | 1 | 132 | 1802 | 1 |
| 158 | 1776 | 1 | 150 | 1784 | 1 | 129 | 1805 | 1 |

Total number of trees—20.      Mean age—152.45 years.

¹ Beginning of period of intensive reoccupation.

² End of period of intensive reoccupation.

purpose. Lumbering was of no consequence in the region until the advent of railroads in 1884. It would seem at least that the origin of the two older stands would antedate any clearing operation of white settlers. Tornado, fire, disease, and insect infestation seem to be the only factors which could account

for this described condition.   Wholly destructive top fires in mature forest, and wholesale destruction of trees by disease and insects have no counterpart in historical records of this region so the weight of evidence is apparently in favor of tornadoes.   Numerous instances of younger more-or-less pure stands of pine in known tornado paths can be found in southern Arkansas and are locally known as " hurricane forests."   In view of the high tornado frequency rate of the southern part of the state it seems not improbable that this factor is functional in explaining the existence of some old stands of pine in this region.

# STUDY OF ARTHROPOD POPULATIONS BY THE METHOD OF SWEEPING [1]

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In studying an ecological community, it is common practise to sweep herbage and to estimate the number of insects per unit of area from the results. A more legitimate use for the collections is to compare those made at different times and so determine population trends. The problem of determining how far sweeping can represent the population of an area and how much sweeping should be taken to represent a given area is considered in this paper. The extent to which the distribution of animals varies from a random dispersion is considered. An estimate of the number of collections necessary to secure a specified degree of accuracy is investigated. Finally, a few observations are made on the technique of sweeping.

## DESCRIPTION OF THE SITUATIONS IN WHICH COLLECTIONS WERE MADE

Most of the field collections for the study were made in a sixty-acre tract of woodland (University Woods) five miles northeast of Urbana, Illinois. In these woods, the dominant trees are hard maple, elm, and white oak. The sweeps were made in situations where there was an extensive, apparently homogeneous, stretch of herbaceous plants. The predominant herbage of the area in which the sweeps were taken is *Hydrophyllum* sp., *Lobelia siphilitica* L., *Carex* sp., and also a few plants of *Aster cordifolius* L.

## METHODS OF COLLECTION

Sweeping was done with an "American" net. This had a handle one yard long, a hoop 12.8 inches in diameter, and a bag 20 inches deep. In collecting, a long semicircular swing was taken. In an examination the sweeps were found to average 100 inches and to have a standard deviation of 9.5 inches. The insects taken in each sweep were stored separately.

Comparative collections were made with a sweep net and by means of the cylinder method. The former were made during the day. The latter collections were made, as nearly as possible, on the preceding or succeeding night.

Cylinder samples were taken with metal drums 16.8 inches in diameter and one foot deep. In these, one end was closed except that it had a small hole in the centre on which there was a threaded cap. In sampling, these cylinders were placed near an undisturbed region which was to be examined.

After a period of at least one hour had elapsed the cylinders were placed smartly over the herbage and immediately pressed down as far as possible. Anaesthetic was then poured in the hole at the top of each cylinder, the cap replaced, and the anaesthetic poured around the sides. After a period of fifteen minutes the ground about the edge of the cylinders was removed five inches below the surface of the surrounding soil. Anaesthetic was again added around the edge and each cylinder left for a period of thirty minutes. The cylinders were then removed gently. As a result columns of soil five inches high were left. This soil was removed and put into bags.

The process of washing soil and examining the screenings proved so laborious and time-consuming that it was only possible to wash three samples of soil from each of the four collections made. Since a longer series of cylinder samples could not be obtained nothing can be said of the distribution of insects from sample to sample. However, for the sweep-collections a long enough series was taken to make possible the application of statistical theory.

## DETAILS OF COLLECTIONS

The main collections were made in the autumn of 1931. The sweeping was done between 12:00 A.M. and 3:00 P.M. The cylinder collections were made from about 8:00 P.M. until 1:00 A.M. The details are as follows:

Site I, 500 feet from western edge of woods and 950 feet from northern edge: October 20—3 sweeps, October 25—3 cylinders, November 1—16 sweeps, November 2—3 cylinders.

Site II, 400 feet from western edge of woods and 500 feet from northern edge: November 4—14 sweeps, November 9—25 sweeps, November 9—3 cylinders, November 13—9 sweeps.

Site III, 1450 feet from western edge of woods and 1150 feet from northern edge: November 22—16 sweeps, November 22—3 cylinders, November 23—24 sweeps.

## EXAMINATION AND IDENTIFICATION OF MATERIAL

Of the animals taken in sweeping the hard-bodied were immediately stored dry in seamless tins and the soft-bodied arachnids, snails, immature insects, and aphids, were put in alcohol. The dry specimens, constituting about three quarters of the catch, were later sorted into species. The alcoholic specimens were not so sorted.

The material taken in cylinder samples was immediately stored at 20° F. It was later put through a Morris soil washer. This had three screens, the finest of which had 3,500 holes per square centimeter. The screenings were next put in a two quart container with twice their volume of water. The suspension was decanted. Fresh water was put in, the container vigorously shaken, and the water again decanted. The lighter material obtained in this way was finally examined in a Petri dish or larger shallow glass vessel against

a black ground and a white ground. The heavier material left by the decantation was found to contain practically no animals. All animals recovered were put up in vials of 80 per cent alcohol. They were ultimately sorted in the same way as the animals taken by sweeping.

## Number of Sweeps Giving the Population of Unit Area

The reasons why estimation of insect population by a sweep census must vary from time to time have been discussed by De Long ('32). Essentially, the catch made in sweeping comprises only some of the insects present in the herbage.

By the cylinder method the entire insect population in the herbage, on the ground, and in the ground, for the area covered is caught. Catches made by sweeping are compared in this paper, with the catch made by the cylinder method, which is taken as a standard. By such a comparison Shackleford ('29) and Smith ('28) estimated the number of sweeps which gave the insect population per unit area.

The magnitude of the fraction, sweep-catch to cylinder-catch, must be affected by the extent to which a species is in layers other than the herbage, as well as by the extent to which individual members escaped collection in sweeping. It would appear that the influence of these two disturbing tendencies must vary for different species at the same time and for the same species at different times. The magnitude of the values of the fraction, sweep-catch divided by cylinder-catch, as found shows to what extent the sweeps took different fractions of the total population of each species at the time the collections were made. It is impossible, from internal evidence, to say which of the two sources of discrepancy was at work.

Of course in the case of some species one has external evidence to explain discrepancies between sweep-catch and cylinder-catch. Thus, *Blissus leucopterus* Say and *Lygus pratensis* L., are only winter residents in the woods. Although typically herbage inhabiting, they were on the ground of the woods when this work was done in the autumn. This effect is seasonal. The same effect may have occurred to a limited extent in connection with a number of species. Thus, *Notoxus talpa* Laf., was taken in far smaller numbers in the sweep samples than in the cylinder samples. As discussed by Gentner ('28) and by G. M. Stirrett (unpublished paper), some species of *Longitarsus* and *Chaetocnema* have a nocturnal habit and hide in the ground during the day. For all such species as these one cannot expect sweeping to give the same results as cylinder methods.

If one must state how many sweep sample catches represent the population of a unit area, it is necessary to make an estimate on the average for various species, knowing that some will be too high and others too low in the final result. For the several species or groups, under consideration, the mean catch per sample (*i.e.*, per sweep or per cylinder) is determined for each site. Next the unweighted means of the means of the various sites are calculated.

Finally the mean catch per sweep and per cylinder is compared.   These calculations are set forth in table I.

TABLE I.   *The occurrence of various species and groups*

| Name | Number of individuals | Site I | Site II | Site III | Mean | Sweep to cylinder |
|---|---|---|---|---|---|---|
| *Blissus leucopterus* Say . . . . . . . . . . | per sweep | .0 | .1 | .2 | .1 | .02 |
| | per cylinder | 2.0 | 12.0 | 3.0 | 5.7 | |
| *Lygus pratensis* L. . . . . . . . . . . . . . . | per sweep | .0 | .0 | .06 | .02 | .02 |
| | per cylinder | .0 | 3.0 | .00 | 1.00 | |
| *Notoxus talpa* Laf. . . . . . . . . . . . . . | per sweep | .2 | .6 | 1.0 | .6 | .36 |
| | per cylinder | 1.0 | 3.0 | 1.0 | 1.7 | |
| *Longitarsus* spp. . . . . . . . . . . . . . . . | per sweep | .6 | .1 | 1.6 | 1.1 | .16 |
| | per cylinder | 14.0 | 3.0 | 3.3 | 6.8 | |
| *Glyptina* spp. . . . . . . . . . . . . . . . . | per sweep | .1 | .1 | .6 | .3 | .13 |
| | per cylinder | 1.5 | 3.0 | 2.3 | 2.3 | |
| *Myodocha serripes* Oliv. . . . . . . . . . . | per sweep | .3 | .2 | .2 | .2 | .10 |
| | per cylinder | 2.0 | 2.0 | 2.0 | 2.0 | |
| *Chrysopa* sp. . . . . . . . . . . . . . . . . . | per sweep | .2 | .3 | .4 | .3 | 1.00 |
| | per cylinder | .0 | 1.0 | .0 | .3 | |
| *Empoasca* spp. . . . . . . . . . . . . . . . . | per sweep | 1.4 | 6.7 | 7.2 | 5.1 | 1.60 |
| | per cylinder | .8 | 8.3 | .7 | 3.3 | |
| Diptera [2] . . . . . . . . . . . . . . . . . . . | per sweep | 3.1 | 1.4 | 6.0 | 3.5 | 3.20 |
| | per cylinder | .7 | 1.0 | 1.7 | 1.1 | |

[2] Among the Diptera, *Leptocera* spp. predominated.   *Drosophila* spp., Cecidomyidae, Mycetophilidae, *Oscinus* spp., Tipulidae, were among the next most common groups in the order given.   These small flies are extremely difficult to separate.   *Lucilia sericata* Meig. was the only large species taken in numbers.

If one neglects the two first species of winter residents one finds an average value of .94 for the fraction of sweep over cylinder.   Since a cylinder had an area of .17 square meters, a sweep caught .16 of the insects from a square meter and about six sweeps represented a square meter.

Exception may be taken to the procedure of combining data from various sites.   To have made a study of each site separately would indeed have been preferable but the collections were not extensive enough to do so.

The weight which the various items should be given is a subjective matter.  Thus, the Diptera, in table I, might have been given the weight of many species, and the general ratio of sweep-catches to cylinder-catches raised.   However, these flies were almost all of very small size, and probably of but little interest ecologically.

The average number of all insects taken in sweeps is given below for each site.   For catch in cylinders, a corresponding average of all insects, less carabids, staphylinids and species believed to be practically confined to the ground, is shown.   The two figures are estimates of the number of insects in the herbage.

| | | Site I | Site II | Site III | Mean | Sweep to Cylinder |
|---|---|---|---|---|---|---|
| Total | Sweeps | 15 | 12 | 21 | 16 | .67 |
| Catch | Cylinders | 25 | 28 | 20 | 24 | |

A sweep, on the above basis, gave .67 times as many insects as .17 square meters, or a cylinder-sample. Accordingly, nine sweeps should contain the animals of a square meter. The discrepancy between this value and the value of six sweeps, previously obtained, lies partly in the fact that Diptera and the leafhopper, *Empoasca,* constituted about two-thirds of the total number of insects taken in sweeping, although they are only given two-sevenths of the weight in table I. Both these groups were much more numerous in the sweeps than in the soil samples. As is shown below, when these groups are subtracted from the total, the ratio between sweep and cylinder samples departs widely from that obtained from table I.

|  | Mean | Sweep to Cylinder |
|---|---|---|
| Total catch minus | 7.4 | .37 |
| *Empoasca* and Diptera | 19.9 | |

Taking the unweighted mean, it is found that a sweep collects .37 times as many insects as one cylinder sample. Therefore sixteen sweeps 100 inches in length, represent the population of a square meter on this basis of insects.

To sum up this discussion, it seems that somewhere between six and nine of the single 100 inch strokes used, indicate, as well as anything, the population of one square meter.

## ARRANGEMENT OF ORGANISMS IN SPACE

The individual organisms of a species or group may be distributed at random, or be arranged by spacing away from one another, or be aggregated. The type of distribution affects the number of samples necessary to secure a given degree of significance to sample values. Also by knowing which type of arrangement obtains for an organism one might interpret the relationship existing between the individuals. The intensity of spacing phenomena can be expressed numerically. When this is done, corresponding tendencies for various organisms may be compared.

Gleason ('20) divides the number of quadrats containing a given species of plant by the total number of quadrats examined. He calls the value obtained the Frequency Index (F.I.) and shows how one may test whether the F.I. is greater or less than would be expected if the individuals present were randomly distributed. That is, he tests whether the distribution of the plants is random. Such a method can indicate departures from random distribution and the direction of departure. This method, however, does not utilize the information on the variation within the occupied quadrats; that is, the information on the number per quadrat of the given species.

The distribution, per small unit of area, holding for objects scattered at random over a wide area is the Poisson series. On this basis the observed distributions may be judged. One may say that the standard deviation of the number of individuals per sweep should be equal approximately to the square root of the mean of the observations, Crathorne ('28).

The observed standard deviation was compared, following Fisher ('30), with the theoretical standard deviation by the two following coefficients of disturbance:

$$\text{Lexis,} \ \frac{s}{\sqrt{x}},$$

$$\text{Charlier,} \ \frac{100\sqrt{s^2 - x}}{x},$$

where $s$ is the calculated standard deviation, $x$ is the mean catch for the group.

The degree of disturbance of organisms of an area is expressed numerically. Of course, in the event of self-spacing, hyponormal values (imaginary values for the Charlier coefficient) would be found; in the event of aggregation or colonization hypernormal values would be found.

The values obtained from sweepings on the two days with the longest series of collections were studied. The results are shown in table II.

TABLE II. *The distribution of individuals per sweep*

| November 9, 1931. Site II. 25 Sweeps. | | | | | |
|---|---|---|---|---|---|
| | $x$ | $s$ | $\sqrt{x}$ | Lexis' Coefficient of Disturbance | Charlier's Coefficient of Disturbance |
| *Empoasca* spp. | 6.72 | 4.17 | 2.59 | 1.61 | 49 |
| *Longitarsus* spp. | 1.24 | 1.53 | 1.11 | 1.38 | 85 |
| *Glyptina* spp. | .48 | .76 | .69 | 1.10 | 62 |
| November 23, 1931. Site III. 24 Sweeps. | | | | | |
| *Empoasca* spp. | 8.00 | 5.31 | 2.83 | 1.88 | 56 |
| *Nabis* sp. | .56 | .77 | .75 | 1.03 | 30 |
| *Longitarsus* spp. | 1.78 | 1.77 | 1.34 | 1.32 | 65 |
| *Glyptina* spp. | 1.30 | 1.23 | 1.14 | 1.08 | 36 |

Table II shows hypernormal values both for Lexis and for Charlier coefficients in every case. Accordingly, the individuals of each group must tend to form aggregations. It appears, as would be expected, that the Lexis coefficient varies with the magnitude of $x$, of which the Charlier coefficient appears to be independent.

## THE NUMBER OF SWEEPS NECESSARY FOR A SPECIFIED DEGREE OF ACCURACY

On the basis of preliminary sampling of a certain population, Gray and Treloar ('33) consider the question of how large a sample one would have to take from that population to obtain a specified degree of accuracy. They measure the degree of accuracy by the coefficient of variation. By increasing the size of the sample the standard deviation of the mean is reduced and its accuracy therefore increased. The procedure of the above-mentioned authors is followed.

Suppose $\bar{x}_k$, an estimate of the mean catch per sweep, has been obtained from a series of $k$ sweeps; and from the same series $s_k$, an estimate of the standard deviation, has also been obtained. It is desired to find $n$, which is the number of sweeps necessary if values of $\bar{x}_n$ shall rarely differ from $m$ by more than the $y$th part of $m$. The symbol $y$ is an arbitrary constant, and $m$ is the true mean of the population. For the purposes of analysis, say $\bar{x}_n$ must be so distributed that it will probably not deviate from the population mean, $m$, by more than $y$ of $m$, oftener than one time in twenty. That is one wishes $2s_{\bar{x}_n}$ to equal $y(m)$.

An estimate of $n$ is sought when $y$ is put equal to .1. The data from table II give, as the number of sweeps necessary, the following results:

|  | Site II | Site III |
| --- | --- | --- |
| *Empoasca* spp. | 154 | 176 |
| *Longitarsus* spp. | 609 | 396 |

Of course the value of $n$ is not exact, only the magnitude is estimated. As $\bar{x}_k$ decreases in size the estimate becomes less accurate.

The values obtained are four times smaller [3] than those obtained by the above-mentioned authors who set excessively severe limits on the behavior of their estimate of $\bar{x}_n$. Even when the same formula is used the results obtained in this work indicate that rather smaller values are necessary for $n$ than the paper of Gray and Treloar suggests. This difference is probably due to mechanical difficulties they encountered in making uniform a series of continuous sweepings, rather than a series of single sweepings.

## The Use of a Square Net

It was thought that a square-mouth net might be substituted profitably for the round-mouth net commonly used in sweeping. It might have been easier to keep the sweep of the former type uniform. Even if the circular net is swung in a constant manner only an arc is moving through the herbage. Square-mouth nets have been used in sweeping dense stands of seaweed in shallow water, Petersen ('13). Also in bottom dredging it is customary to collect with a rectangular shaped receptacle.

A net was tried with a square wire "loop" having the handle set on one

[3] There was a slight confusion in the original paper which is being corrected at the time of writing by A. E. Treloar. The formula used in our paper is $n = \dfrac{4 s_k^2}{y^2 \bar{x}_k^2}$. Gray and Treloar give the formula $n = \dfrac{16 V^2}{y^2}$ in which $V$ is the coefficient of variation $\left(\dfrac{100 s_k}{\bar{x}_k}\right)$ and $y$ is the percentage of the mean within which as a range, 95 per cent of the means of the samples are to fall. Our $y$ is the fraction of the mean within which as a deviation above or below the mean, 95 per cent of the means of samples are to fall. Their $y$ is thus 200 times our $y$. With these substitutions the two formulae are identical.

corner at an angle of 135° to the adjacent sides of the "loop." This arrangement has the advantage that, if one mark a place on the handle and hold it there and then keep the bottom of the net parallel with the ground, one automatically keeps a very nearly constant radius to his swing.

Some experimental sweeping was done in a field of alfalfa to test the relative advantage of the two shapes of net. These were made with the same area of "loop." A single sweep was made with one type of net and the catch of *Lygus pratensis* L. noted. Three paces were then made forward and a sweep with the alternative type of net made. This alternation was continued. Sweeping was done across a light wind. The results were as follows:

| Date | Number of sweeps | Height of alfalfa | Square-mouth net | | Round-mouth net | |
|------|------------------|-------------------|:----:|:----:|:----:|:----:|
| | | | *x* | *s* | *x* | *s* |
| Aug. 14, 1933 | 30 | 9 inches | 1.10 | .94 | .97 | .98 |
| Aug. 21, 1933 | 30 | 14 inches | .80 | 1.04 | .73 | .96 |

No difference in the results from the two types of net was apparent. However, it was easier in the case of the square-mouth net to maintain a constant radius of swing.

### RECORDING BY INDIVIDUAL SWEEPS

All through this work the records have been of individual sweeps rather than of the usual massed sweeping of ecologists. The former procedure has the advantage that one can establish an estimate of reliability on an area which by massed sweeping would only give an estimate of average value. Also, if one should wish to make a study of population against time he could use a smaller region and so escape some heterogeneity of data. Single strokes possess one serious disadvantage as pointed out by De Long ('32). "A more representative population sample is obtained by two strokes over the same vegetation" since the first stroke rouses the insects and the second stroke takes them.

One may suppose that frequently, in the field, the density of population of a species of insects changes as one moves constantly in a given direction. One may say there is a spacial gradient for the population. When one takes the first twenty-five sweeps as one sample, the next twenty-five as a second sample, and so forth, the observed variability consists in part of this spacial trend. For some purposes one might profitably take single sweeps and combine, say the first, twelfth, twenty-third, etc., as one sample, and equally scattered sweeps as a second sample, and so forth. One could thus obtain samples with the spacial variability eliminated. Such procedure was followed by Haig ('29) in his studies on distribution of seedlings.

## Applications of Sweeping Apart from Estimation of Population

Sweep samples which give only a poor estimate of the population of an area may still be useful as indicators of various population phenomena. Thus seasonal fluctuations in the size of population have been determined without knowing the actual size of the population. Also aggregation might be demonstrated by the extent of variation from sweep to sweep even if the results gave no estimate of the total population present.

## Summary of Conclusions

The estimates of insect population from cylinder collections and from sweep collections are essentially based on different populations. For the calculation of population of any species or group of an area, from sweeping data, a different conversion factor should be used for each species. Somewhere between six and nine of the single 100 inch strokes used indicate, as well as anything, the population of one square meter. The insects studied all showed greater variability in frequency per sweep than if they had been randomly distributed. Charlier's coefficient is probably the best index for measuring phenomena of such disturbance. The method suggested by Gray and Treloar of estimating the number of sweeps necessary for a specified degree of accuracy with a correction of their original formula is followed. The data of this paper suggest rather fewer sweeps to be necessary in order to obtain a specified degree of accuracy than the data they collected. A square-mouth sweep net, rather than the usual round-mouth, was employed without any substantial advantage. It is pointed out that on theoretical grounds single sweeps, rather than continuous sweeps, may be profitable.

## Acknowledgments

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# AN ECOLOGICAL RECONNAISSANCE IN THE WHITE SANDS, NEW MEXICO

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The White Sands occupy an area located in the desert in a westerly and southwesterly direction from Alamogordo, New Mexico. This area, unlike the ordinary dune, which is of quartz sand, consists of drifting crystals of gypsum.

A search of the literature reveals few ecological studies in these sands. The only article found that deals with plant ecology is a brief account contained in a report by Coville and MacDougal ('03), in which these botanists describe the physical conditions, list some of the more important species of
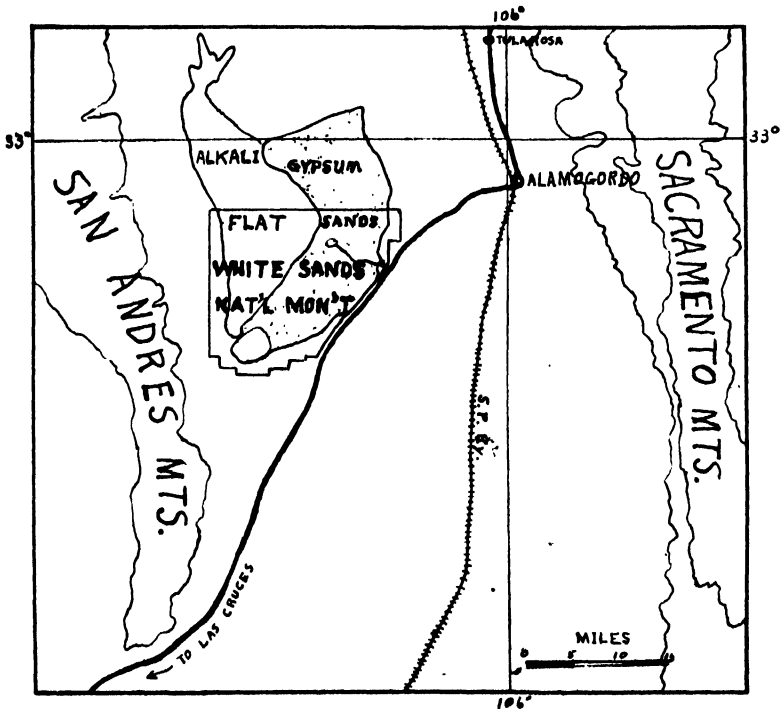


FIG. 1. Map of environs of White Sands near Alamogordo, New Mexico.

plants, and include a chemical analysis of the sand. Dice ('30) and Benson ('33) have published important papers in which they contrast the colors of mammals of the White Sands with those of the near-by dark terrain.

The study reported here deals with peculiarities of plant distribution in the White Sands and is based on two periods of work, March 30 to April 7 and June 30 to July 3, 1934.

## PHYSICAL AND CHEMICAL DESCRIPTION

The White Sands, proper, occupy an area of approximately 270 square miles. Adjoining the dunes on the west and extending to the lower foothills of the San Andres Mountains there lies an area usually indicated on maps as an alkali flat (fig. 1). This area is covered to an unknown depth with a crusted, non-drifting deposit. Those who live in the region report that at times of wet weather this flat becomes covered with a foot or more of water. The place is usually considered to be an ancient lake bed (fig. 2). On the north, east, and south sides, the dunes border on the desert plains of the region.

The dunes, when dry, are brilliant white, giving the impression of gigantic snow drifts (fig. 3). In the flats between the active dunes the sand is stained a very pale yellowish-brown color. The powerful effects of the combined actions of the direct sunshine under the usually cloudless skies of this desert climate with the extreme reflection from the sands needs study. It is obvious, however, that plant protoplasm must meet unusual conditions of light. Both the much-shortened photographic exposure and sunburn of hands and face even when protected from the direct rays of the sun attest to the powerful radiant energy which is reflected from all directions.

The crystals that compose the dunes are chiefly of gypsum, a very soft mineral. The sands can be ground to almost flour-like fineness between the fingers, and they possess a relatively high solubility. All water absorbed by roots in the gypsum sands must be taken from a practically saturated solution of calcium sulphate.

In order to determine the growth water of the sands, samples were taken from five different localities and dried to determine water-supplying power, care being exercised not to use enough heat to drive off the water of crystallization of the gypsum. Those samples taken from the surface of the top of a dune; from six inches below the surface on a windward slope; from six inches below the surface on the leeward side of a dune; and from the upper inch of sand on a flat where vegetation was growing vigorously, all showed no loss of water when placed in conditions for drying. Of all the localities tested, only one, six inches below the surface on a flat, contained growth water. This was at the level of most of the roots. This sample contained 2.2 per cent of water calculated in terms of dry weight of the sand. The wilting coefficient of the sand as determined by the permanent wilting of wheat was 0.8 per cent of the dry weight of the sand. Therefore the sand contained 1.4 per cent of growth water. The water table was between 2 and 3 feet below the surface in these flats. No opportunity was afforded to make extensive studies of the evaporating power of the air, but some slight infor-

mation was gotten from two standardized, white, cylindrical atmometers allowed to run over a period of 21.5 hours from the evening of June 30 to the afternoon of July 1. One was set on top of an advancing dune. The corrected reading was 61.4 cc. The other was set at the foot of the leeward face of the same dune. The corrected reading in this instance was 46.8 cc. or 76 per cent as much as that in the exposed position.



FIG. 2. (Above.) Alkali flat adjacent to White Sands. *Allenrolfia occidentalis* in foreground.
FIG. 3. (Below.) White Sands, looking toward San Andres Mountains. Desert vegetation in the flats between dunes.

Maximum and minimum temperatures were taken in April and again in July. Table I records the results:

TABLE I.  *Maximum and minimum temperatures*

| Dates | Position | Maximum °F. | Minimum °F. | Temperature range °F. |
|---|---|---|---|---|
| April 2 | Air | 78 | 44 | 34 |
| April 3 | 6 in. in sand | 56 | 48 | 8 |
| April 4 | Air | 74 | 36 | 38 |
| July 2 | Air | 100 | 58 | 42 |

As a supplement to these records comparative temperatures of sand and air were taken in both the alkali flat and the dunes on July 1 with the following results:

TABLE II.  *Temperatures in dunes and alkali flat in mid-summer*

| Location | Hour | Air °F. | In sun; on sand °F. | 1 in. deep °F. | 7 in. deep °F. |
|---|---|---|---|---|---|
| Alkali flat | 10:00 a.m. | 93 | 108 | 93 | 77 |
| Dunes | 4:30 p.m. | 99 | 108 | 99 | 81 |

The most complete chemical analysis to which I have had access is contained in the report by Coville and MacDougal ('03) in which the composition is given as, gypsum, $CaSO_4 \cdot 2H_2O$, 95.8 per cent; $SiO_2$, 2.7 per cent; $Al_2O_3$ and $Fe_2O_3$, 0.4 per cent; traces O, Cl, Na, and $PO_4$.  The statement of these authors that, " Such organic matter as was actually present in the few particles separated from the sand consists . . . of fragments of insects, excreta of animals, etc. and is too slight in quantity to have much significance as nutrient material for plants," raises the question of the source of nitrogen used in the metabolism of the plants.  Recent tests for total nitrates and nitrites made by Dr. O. B. Muench from sand taken from a flat in the immediate vicinity of roots where the vegetation was relatively luxurient showed a concentration of only 0.0008 per cent, thus largely substantiating the earlier reports.  The only clue to a possible solution of the problem of the nitrogen supply of plants rooted in the sand comes from a preliminary examination of the roots of *Yucca elata*.  These roots have well developed endotrophic mycorhizas.  It is possible that the fungi involved may fix nitrogen and thus supply that element to the yuccas.  Other plants have not yet been examined for mycorhizas.  A thorough study of nitrate distribution and of mycorhizas might throw a considerable amount of light on the peculiar distribution of plants to be discussed in the section following.

## PLANT DISTRIBUTION

According to Wooton and Standley ('15) 57 species of seed plants are to be found in the White Sands.  Of these, two are endemics.  Five species not specifically mentioned as coming from the White Sands are known by the writer to be represented, thus making a species population of at least 62.  Standley ('10) cites 9 species that were first named from materials collected in the White Sands, although some of these have wide distribution.

TABLE III. *List of species known to grow in the White Sands, classified as to distribution. Nomenclature from Wooton and Standley*

|  | Wide Dist. | Local Desert | Endemic |
|---|:---:|:---:|:---:|
| Ephedraceae |  |  |  |
|   *Ephedra torreyana* S. Wats. | + |  |  |
| Poaceae |  |  |  |
|   *Schizachyrium neomexicanum* Nash |  | + |  |
|   *Aristida bromoides* H.B.K. | + |  |  |
|   *Muhlenbergia pungens* Thurb. | + |  |  |
|   *Oryzopsis hymenioides* (Roem. & Schult.) Ricker | + |  |  |
|   *Sporobolus giganteus* Nash |  | + |  |
|   *S. auriculatus* Vasey |  | + |  |
|   *S. asperifolius* (Nees & Mey.) Thurber | + |  |  |
|   *S. airoides* Torr. | + |  |  |
|   *S. nealleyi* Vasey |  | + | • |
|   *S. flexuosus* (Thurb.) Rydb. | + |  |  |
|   *Bouteloua barbata* Lag. | + |  |  |
|   *B. breviseta* Vasey |  | + |  |
|   *Distichlis spicata* (L.) Greene | + |  |  |
| Juncaceae |  |  |  |
|   *Juncus mexicanus* Willd |  | + |  |
| Dracenaceae |  |  |  |
|   *Yucca elata* Engelm. |  | + |  |
| Salicaceae |  |  |  |
|   *Populus wislizeni* (S. Wats.) Sarg. | + |  |  |
|   *Salix nigra* Marsh | + |  |  |
| Chenopodiaceae |  |  |  |
|   *Dondia suffrutescens* (S. Wats.) Heller |  | + |  |
|   *D. moquini* (Torr.) A. Nels. | + |  |  |
|   *Allenrolfea occidentalis* (S. Wats.) Kuntze | + |  |  |
|   *Atriplex canescens* (Pursh) Nutt. | + |  |  |
| Allioniaceae |  |  |  |
|   *Abronia angustifolia* Greene |  |  | ǀ |
|   *Selinocarpus lanceolatus* Wooton |  | ǀ |  |
| Brassicaceae |  |  |  |
|   *Nerisyrenia linearifolia* (S. Wats.) Greene |  | ǀ |  |
| Euphorbiaceae |  |  |  |
|   *Chamaesyce serrula* (Engelm.) Woot. & Stand. |  | ǀ |  |
| Anacardiaceae |  |  |  |
|   *Schmaltzia emoryi* Greene |  |  |  |
|     *Rhus trilobata mollis* A. Gray | + |  |  |
| Malvaceae |  |  |  |
|   *Sphaeralcea arenaria* Woot. & Standl. |  | + |  |
|   *S. cuspidata* (A. Gray) Britt. | + |  |  |
|   *S. incana* Torr. |  | + |  |
|   *Disella lepidota* (A. Gray) Greene |  | + |  |
| Frankeniaceae |  |  |  |
|   *Frankenia jamesii* Torr. |  | + |  |
| Loasaceae |  |  |  |
|   *Nuttallia procera* Woot. & Standl. |  | + |  |
|   *N. multiflora* (Nutt.) Greene | + |  |  |
| Cactaceae |  |  |  |
|   *Echinocereus gonacanthus* (Engelm. & Bigel.) Lem. |  | + |  |
| Epilobiaceae |  |  |  |
|   *Galpinsia filifolia* (Eastw.) Woot. |  | + |  |
|   *Anogra gypsophila* (Eastw.) Heller |  |  | + |
| Gentianaceae |  |  |  |
|   *Centaurium texense* (Griseb.) Fernald |  | + |  |
|   *Eustoma russellianum* (Hook.) Griseb. | + |  |  |

TABLE III. *(Continued)*

| | Wide Dist. | Local Desert | Endemic |
|---|---|---|---|
| Asclepiadaceae | | | |
| *Asclepias arenaria* Torr. | | + | |
| Convolvulaceae | | | |
| *Ipomoea hirsutula* Jacq. | | + | |
| Polemoniaceae | | | |
| *Gilia pumila* Nutt. | + | | |
| Hydrophyllaceae | | | |
| *Andropus carnosus* (Wooton) Brand | | + | |
| *Phacelia corrugata* A. Nels. | + | | |
| Ehretiaceae | | | |
| *Eddya hispidissima* Torr. | + | | |
| Verbenaceae | | | |
| *Phyla incisa* Small | | + | |
| Menthaceae | | | |
| *Poliomintha incana* (Torr.) A. Gray | + | | |
| Solanaceae | | | |
| *Lycium parviflorum* A. Gray | | + | |
| Cucurbitaceae | | | |
| *\*Cucurbita foetidissima* H.B.K. | + | | |
| Mutisiaceae | | | |
| *Perezia nana* A. Gray | | + | |
| Asteraceae | | | |
| *Chrysothamnus pulchellus* (A. Gray) Greene | + | | |
| *C. latisquameus* (A. Gray) Green | | + | |
| *Sideranthus spinulosus* (Pursh) Sweet | + | | |
| *Isocoma heterophylla* (A. Gray) Greene | | + | |
| *Machaeranthera parviflora* A. Gray | | + | |
| *M. linearis* Greene | | + | |
| *Dicranocarpus dicranocarpus* (A. Gray) Woot & Stand. | | + | |
| *Crassina grandiflora* (Nutt.) Kuntze | + | | |
| *\*Thelesperma gracile* (Torr.) A. Gray | + | | |
| *Psilostrophe tagetinae* (Nutt.) Britt. & Brown | + | | |
| *Clippia suaedifolia* A. Gray | | + | |
| *Hymenopappus arenosus* Heller | + | | |
| *Sartwellia flaveriae* A. Gray | | + | |

Table III is compiled from Wooton and Standley, Flora of New Mexico, using their nomenclature and statements of species distribution. The species marked * are known to thrive in the White Sands although their presence is not mentioned by Wooton and Standley.

Those species that extend their distribution into more than one life zone are considered to be of wide distribution; those that are limited to the desert of southern New Mexico, Texas, and Arizona are listed as plants of the local desert; and the two endemics are limited to the White Sands proper.

The most complete studies of plant distribution I was able to make took the form of a wide belt extending from the leeward margin of the advancing dunes on the east to a point perhaps two miles within the alkali flat at the western margin of the dunes, a distance of about 12 miles.

Most of the species are limited to the flats between the active dunes nearest to the general desert, some entering only a few rods while others penetrate far inward. Numbers of both species and individuals gradually decrease with increasing distances from the general desert. See table IV.

Individuals of 7 species are able to grow upward through the encroaching

Fig. 4. White Sands encroaching on desert. Several species are elongating and preventing destruction by drifting sand.

sands and to produce adventitious roots when their stems are covered (fig. 4). The following table indicates the approximate distance each of these species has penetrated into the dunes from the desert and the greatest height attained when covered by dunes:

TABLE IV. *Distances of penetration from the desert into the White Sands of some important species, with greatest height observed when covered by dunes*

| Species | Dist. of penetration in miles | Normal height, ft. | Ht. covered by dunes, ft. |
|---|---|---|---|
| *Ephedra torreyana* | 10 | 3–4 | 20 |
| *Yucca elata* | 7 | 15–20 | 40 |
| *Populus wislizeni* | 4 | large tree | 60 |
| *Atriplex canescens* | ¼ | 2–3 | 40 |
| *Schmaltzia (Rhus) emoryi* | 2 | 4–5 | 50 |
| *Poliomintha incana* | 5 | 3 | 40 |
| *Chrysothamnus latisquameus* | 7 | 3 | 20 |

There is no evidence of any reproduction of any plant except in the flats. The motion of the sand and the lack of available water in the superficial layers of the active dunes conspire to prevent the growth of seedlings. In the flats, however, seedlings and mature, fruiting plants are very numerous wherever the vegetation has penetrated. Because the plants are rooted in the flats it is possible to determine accurately the total height of plants that are partly covered by dunes.

At a distance of 7.5 miles within the dunes in the region studied there are

only three species. They are *Ephedra torreyana* which extends from the desert to within one-fourth mile of the alkali flat; sand bunch grass, *Oryzopsis hymenioides,* which has reached a point about one and one-half miles from the alkali flat; and sand verbena, *Abronia angustifolia,* an endemic whose distribution seems to be limited to the alkali flat and White Sands. A plantless zone about one-fourth mile wide in the western border of the dunes separates the vegetation of the dunes from that of the alkali flat.

In the alkali flat there are representatives of only two species of plants. These are scattered individuals of sand verbena, *Abronia angustifolia* and of burro weed, *Allenrolfea occidentalis* (fig. 2).

## SUMMARY

1. Studies were made of the vegetation of the White Sands in spring and summer of 1934.

2. Plants seem to be in the process of migrating from outside sources into the dunes with the possible exceptions of two endemics that may have originated within the area. Some species have entered only a short distance while others have migrated several miles.

3. No seedlings establish themselves except in the flats, between the moving dunes.

4. In the flats soil water is near the surface, the water table being between 2 and 3 feet deep with moist sand reaching almost to the surface.

5. Roots must absorb water from a saturated solution of calcium sulphate.

6. Even in the most luxurient stands of plants there is a very slight concentration of nitrates and nitrites, thus raising the question of methods of nitrogen assimilation.

7. Seven species have the power to grow upward rapidly enough to survive encroaching sand. All of these produce adventitious roots when covered. At least 55 species are limited to the flats because they can not elongate when covered.

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# A STUDY OF THE COMMUNITY RELATIONSHIPS OF THE SEA MUSSEL, *MYTILUS EDULIS* L.

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## INTRODUCTION

A study of the major intertidal communities of the Bay of Fundy has indicated variations in vertical distribution of *Mytilus edulis* within the widely separated regions observed. Whereas mussel communities of considerable size occur at levels below the mean low water level (M. L. W. L.) on the Nova Scotia side of the Bay, those in the St. Andrews region (New Brunswick side) are almost entirely confined to the intertidal zone. This pronounced difference in vertical distribution has suggested the problem of determining why extensive submerged mussel communities do not grow in St. Andrews waters. Attention to this phenomenon of distribution is warranted in light of the findings of Mossop ('22) which show that the most rapid growth rate, under experimental conditions, occurs when specimens are always submerged at a depth of one foot below the water surface.

The writer's interest in this particular problem was aroused through observations made by Professor A. G. Huntsman pertaining to the limitation of mussel distribution on wharf pilings at the Atlantic Biological Station. It was suggested that this phenomenon might be due to the predatorial influence of starfishes and sea urchins. To determine the validity of this explanation the present study was undertaken and has included an analysis of some of the important community relations of *M. edulis* since it was believed that certain of these biotic interactions explain the limited downward distribution of the mussel in the St. Andrews region.

Data accrued pertain firstly, to the dominant and influent organisms as well as those of secondary importance in the *Balanus-Mytilus edulis* Association (Newcombe, '35), and secondly, to the seasonal growth rate of *Mytilus* during 1931.

In an attempt to evaluate the relative degrees of influence possessed by the animals and plants of this association of which *M. edulis* is a dominant, we have followed the community nomenclature of Shelford [1] with modifications (compare Newcombe, '35). For the reader's convenience the terms are defined here.

[1] Personal communication.

*Dominants* control the habitat biota, being of outstanding abundance or conspicuous influence in the community throughout the entire active or growing season.   On land they are usually plants whereas in salt and fresh water, animals most often dominate.

*Codominants* are dominant plants occurring among several dominant animals and present during the entire growing season.

*Subdominants* have important influence in the control of the life of the habitat, but are usually present only a part of the active or growing season.

*Influents* are common forms which have important relations in the biotic balance and in the community.   They affect: (*a*) the bodily well-being of certain sessile forms such as conspicuous plants (*e.g. Fucus* and *Ascophyllum*) by predatorial action; or (*b*) the number of associated organisms without altering the essential composition of the biotic community or markedly changing the rate of succession; or (*c*) the abundance of food.

*Subinfluents* exert a lesser influence.   Normally, they are present during only a part of the year.

*Secondary forms* are considered to be those of minor influence in the community.   They usually occupy a narrow range or a local habitat and occur in relatively small numbers.

A *biotic community* is an assemblage of relatively uniform taxonomic composition and physiognomy.

A *habitat* is an area occupied by a community, the life of which is controlled by climate, soil, substratum or water.   There are two types of habitats recognizable: (1) the major habitats such as grassland, or deciduous forest, on land and sand, or rock habitats on the sea shore, all of which are extensive; (2) the local habitats determined by soil, water, or illumination, and usually occurring locally within the major habitats and constituting breaks within them.

On account of the limited knowledge pertaining to the inter-relations of the constituent organisms of a biotic community, ecologists have clung quite tenaciously to numbers as criteria of degree of influence.   It is with the desire of somewhat improving this basis in regard to the community relations of *M. edulis* that this study has been pursued.

Thus far, workers in the field of community ecology have largely confined their efforts to inland communities where pristine conditions are often exceedingly difficult to obtain.   On a basis of the results thus secured, questions such as the relative importance of plants and animals in a biotic community (on which problem opinion is still by no means unanimous) are being answered (Phillips, '31).   It seems evident that the marine environment especially the intertidal zone, has much to offer the student of animal populations, relationships which may go a long ways toward settling numerous and much debated present-day problems.

## METHODS

The methods of community analysis employed were designed for estimating relative abundance of the more conspicuous animals and plants and for the purpose of interpreting certain biotic interrelationships throughout all sea-

sons of the year.    In the population study, vertical transects were made across the intertidal zone and, within these, permanent quadrats, each 10 square meters in area, were selected for intensive study at the desired levels.

For determining the extent of growth in nature, mussels were planted on the beach in experimental boxes at levels of 3 feet and 10 feet above chart datum.    The boxes possessed a solid wooden frame covered with a wire screening of 5 mm. mesh, their dimensions being 30 x 30 x 20 mm. (depth). Each box was provided with a cover also of wire screening.    In the experiments an effort was made to simulate natural conditions while providing a protection for the experimental animals against predators.

## RESULTS

### *The Balanus-Mytilus edulis Association*

The sea mussel meets the requirements for dominant rank in this community being present in relatively large numbers throughout all seasons of the year and exerting a marked influence on the physico-chemical and biotic environments.    In the spring season, numbers as high as 4,000 per meter square area with average length of 18–22 mm. frequently obtain.    Later, due to growth with consequent crowding out of young specimens and also due to predatorial influence, the numbers are substantially reduced.    There frequently remain numbers averaging around 700 per meter square area (average length 55–60 mm.) which form a quite uniform layer over the beach surface. At this stage conditions are favorable for the establishment of several epifaunal animals and plants, thus demonstrating the occurrence of true succession in the intertidal community (compare Shelford, '30).    Accompanying an increase in age, the community becomes distinctly more integrated with respect to the interaction of the constituent biota.    Subsequently, a state of balance is reached and seemingly maintained, the breaks within the association usually being filled each year by sets.    The establishment and development of this community greatly modifies the habitat (*e.g.*, changes the porosity of the soil and sulphide content), thus favoring the introduction of certain infaunal forms and driving out others such as the soft-shelled clam, *Mya arenaria*, of the *Mya-Nereis virens* Biome (Newcombe, 1935):

Results of observations favor attributing to the community associates of *M. edulis* the ranks listed below.

Dominants—*Balanus balanoides, Littorina litorea.*
Codominants—*Fucus vesiculosus, Ascophyllum nodosum.*
Subdominants—*Littorina rudis, Purpura lapillus.* ·
Influents—*Gammarus* (3 species), *Littorina palliata.*
Subinfluents—*Lunatia heros, Acmaea testudinalis, Buccinum undatum.*
Secondary forms [2]—*Tonicella marmorea, Sertularia* sp., and other hydroids.

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[2] I am indebted to the late Professor A. Brooker Klugh for numerous identifications.

Additional forms including invaders are:

Animals—

Alcyonidium sp., an encrusting bryozoan obtained at depth of 3 fathoms.

*Chrysidomus decemcostatus*—locally distributed just below the M. L. W. L.

*Modiolaria discors*—occasionally found at depth of about one fathom during M. L. W. L.

*Saxicava rugosa*—not common.

*Pagurus* sp.—occasionally observed below M. L. W. L.

*Boltenia* sp.—frequently found fastened to mussels growing below M. L. W. L.

*Tubularia crocea, Metridium dianthus, Cucumaria frondosa, Lophothuria fabricii, Anomia* sp., *Strongylocentrotus drobachiensis, Crossaster papposus, Asterias vulgaris, A. forbesii, Henricia sanguinolenta.*

Plants---

*Ulva lactuca, Monostroma fuscum blyttei, Spongomorpha arcta, Illea fascia, Scytosiphon lomentarius, Chorda filum, Agarum Turneri, Fucus platycarpus, Chondrus crispus, Lithothamnion polymorphum, Gigartina mamillosa, Rhodymenia palmata, Ptilota serrata, Polysiphonia fastigiata, Delesseria sinuosa.*

The secondary as well as certain of the additional forms listed above are present usually in relatively small numbers and often in restricted areas; hence, their influence in the association is usually slight and they mainly indicate degree of development and integration of the community.

The several dominants and influents are treated separately, as follows:

*Balanus balanoides* is a very abundant (3,000–5,000 per meter square area in August, 1930) and conspicuous constituent of this association, making great demands on the planktonic food supply. Its size and growth form is greatly influenced by radiation.[3] The dogwhelk, *Purpura lapillus,* constitutes an important predator throughout its vertical range.

*Littorina litorea* by virtue of high numbers throughout all seasons, its wide vertical distribution in the community and its probable influence on the community associates through food relations (*Balanus balanoides, Fucus vesiculosus, Ascophyllum nodosum,* diatoms) has been assigned dominant rank.

*Littorina rudis* is a subdominant occurring throughout all seasons in numbers as high as 500 per meter square area. It is most abundant between levels of 14 and 20 feet above chart datum. In winter, its distribution is noticeably localized due to adverse temperature conditions which cause aggregations in protected areas, *e.g.,* under stones, in crevices and under algal growths.

*Purpura lapillus* exerts a very important effect on the community due to predatorial influence. Although not usually present in very great numbers

[3] Klugh, A. Brooker, and Newcombe, Curtis L.—unpublished data.

(frequently numbers ranging from 20 to 40 per meter square area have been obtained) they alter the community aspect by destroying barnacles and mussels in large numbers. In view of this fact and by virtue of their wide vertical distribution throughout the entire active or growing season (they may move down to the lower levels in winter), we have assigned to them subdominant rank.

*Asterias vulgaris, A. forbesii* and *Strongylocentrotus drobachiensis* are important predators, being invaders from the subtidal *Strongylocentrotus-Asterias Biome*. Their effect is, however, chiefly confined to the lower limits of the community since they seldom range for any considerable distance above the M. L. W. L. *S. drobachiensis* and *Purpura lapillus* are destructive to barnacles and sea mussels. One thousand empty mussel shells (length range 20–55 mm.) were closely examined in an effort to evaluate the predatorial influence of the sea urchins, whelks and starfishes. Seventy per cent of the valves bore no marks which might indicate the organism responsible for death. On the basis of numerous field observations, we believe that a large number of these were killed by starfishes. Approximately 20 per cent were cracked and broken along the edges, especially near the posterior end, representing the action of sea urchins, and about 8 per cent showed borings of *Purpura lapillus*. Klugh ('24) has shown that sea urchins definitely limit the downward distribution of Carrigean Moss, *Chondrus crispus*.

*Buccinum undatum* and *Lunatia heros*—Shells containing holes bored by these forms were only occasionally found. This fact, together with their relatively small numbers, warrants their recognition as subinfluents.

*Acmaea testudinalis* is quite a conspicuous member of the community throughout all seasons (it migrates to the lower levels in winter), but, as far as we know, it is only of subinfluent rank.

*Gammarus annulatus, G. marinus* and *G. locusta*. Amphipods are very abundant during all seasons and quite regularly distributed except in winter, when aggregations are frequently found seeking shelter under stones and algal growth. They feed on living and dead animal and plant tissue. Numerous bottom feeding fish use them for food, hence they play an important rôle in the economy of the intertidal zone.

*Fucus vesiculosus* is perhaps the most widely spread and conspicuous alga of the intertidal zone, ranging from M. L. W. L. to as high as 15 or 16 feet above chart datum. It grows intermixed with *Ascophyllum nodosum* throughout a large portion of its range. Intimately associated with it during all seasons of the year are numerous *Littorina* which obtain food and shelter, particularly in winter. By virtue of its importance as a source of food and protection and also because of its wide distribution and conspicuousness throughout all seasons, it has been assigned codominant rank in the *Balanus-M. edulis* Association.

*Ascophyllum nodosum.* This perennial coarse wrack is of wide extent on the intertidal zone. Intimately associated with it are numerous forms, such

as *Littorina* and *Mytilus* that furnish examples of the interaction of plants and animals. A brackish species of the Florideae, *Polysiphonia fastigiata*, is a very conspicuous macroscopic epiphyte frequently found on *Ascophyllum nodosum*. An interesting relationship is revealed in the case of the young forms of *M. edulis* which dwell within the air vesicles of this alga. The growing valves cause the tissues to split and result in the formation of a gall. The bryozoan *Mogula* sp. is frequently found growing on the fronds of *Ascophyllum* and *Fucus*.

## Biotic Interaction

The above remarks concerning members of the *Balanus-Mytilus edulis* Association and more particularly the immediate community associates of the sea mussel illustrate community interaction. Weaver and Clements ('29), working with inland habitats emphasize *food* rather than physical and chemical factors in controlling animals and thereby lending unity to a biotic community. On the intertidal zone this relation does not necessarily obtain. Marine plants constitute not only food but a substratum and a protection against extreme conditions of light and temperature; animals modify physical and chemical conditions of the habitat and make possible the attachment of other animals as well as plants.

The modifying influence of animals on the habitat and their rôle in determining succession and development is illustrated by *M. edulis*. Mussels are able to become established over ground on which the common green alga, *Ulva lactuca*, cannot find anchorage. They provide a suitable foundation for the attachment of *Ulva* as well as other plants and certain animals, such as Cirripedes and Ascidians. The mussel bed clearly illustrates competition within a species. Frequently these occur so abundantly, growing upon one another, until they are several layers deep, that they actually poison and smother one another by the accumulation of waste products and the retention of silt. The soil substratum is thus highly modified, resulting often in the death of certain dominants such as *Mya arenaria* of the *Mya-Nereis virens* Biome (Newcombe, '36). It is apparent, therefore, that the unity of the plant-animal community first pointed out by Shelford ('12) in his study of inland communities, is a reality in the marine habitat.

At this point, attention is called to the striking interaction between *M. edulis* and its predators reported in the preceding pages, which seemingly results in an abrupt limitation of the distribution of mussels below the M.·L. W. L. To strengthen this belief, which is strongly supported by the work of Mossop ('22), who obtained maximum growth rate for mussels continuously submerged one foot below the surface, specimens were planted in experimental boxes designed to simulate natural conditions (except for the protection afforded against predators) at a distance of 3 feet below M. L. W. L. (about 2 feet above chart datum). ''

## Growth of Mytilus edulis

The purpose of our experiments has been, first, to ascertain the growth rate, if any, below M. L. W. L. in areas where mussels are absent and thereby to throw more evidence on the hypothesis that the general absence of mussels below this mean level is due, not to unfavorable conditions for growth, but rather for survival against the natural predators outlined above; secondly, we have endeavored to add to existing information pertaining to the length of the growing season and differential seasonal growth rate.

Two experiments, Boxes " A " and " B," were set up at St. Andrews, N. B. on March 1, 1931, and continued until December 3. Each experimental box contained 45 specimens possessing a mean length of 9.2 mm. (range of length 7.8–10.8 mm.) at the beginning of the experiments. The standard errors of the means and standard deviations were thus kept well within the range of insignificance (table III). Throughout the year, the boxes were removed at times designated in table II and length measurements of the mussels made. Dead specimens, which never exceeded 5 per cent, were discarded and replaced by normal individuals of the desired length. Box " A " was placed in that part of the intertidal zone only exposed during low tides (approximately 3 feet above chart datum), whereas Box " B " was located about 10 feet above chart datum and hence exposed for several hours each day.

*Results.*—Table I shows that the increase of length during the growing season of 1931 (Box " A "—low level) was 16 mm., equivalent to a percent-

TABLE I. *Increments of seasonal growth of M. edulis used in experiments of 1931*

| Box | Level | I. L. in mm. | A. I. in mm. | P. A. of length during "spring" | A. I. of "summer" growth in mm. | P. A. of length during "summer" | A. I. of "fall" growth in mm. | P. A. of length during "fall" | A. I. of "late fall" growth in mm. | P. A. of length during "late fall" | Total A. I. for 1931 | Total P. A. during 1931 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| "A" | 3 | 9.2 | 5.1 | 55.4 | 4.9 | 34.3 | 4.0 | 20.8 | 2.0 | 8.6 | 16.0 | 173.9 |
| "B" | 10 | 9.2 | 4.6 | 50.0 | 3.1 | 22.5 | 3.0 | 17.7 | 1.4 | 7.0 | 12.1 | 131.5 |

I. L.    Initial length.
P. A.    Percentage addition.
A. I.    Absolute increment.
Level expressed in feet above chart datum.

age addition of 173.9 (initial length 9.2 mm.). The percentage increment obtained for the so-called " spring " season was 55.4 mm. (I. L. 9.2 mm.), for the " summer " period 34.3 (I. L. 14.3 mm.) and for the " fall " season 20.8 (I. L. 19.2 mm.). On account of the small growth during the 50-day period following October 14 (" late fall " season), we may reasonably conclude that growth practically ceases late in November, especially in view of the low daily temperatures which obtain at this time (table II). Maximum growth at this

TABLE II. *Seasons, their duration and temperature,[4] during experiments of 1931 in the St. Andrews region*

| Seasons | Duration of seasons | Number of days | Mean daily temperature °C. | |
|---|---|---|---|---|
| | | | Water | Air |
| "Spring" | | | | |
| Total period | March 1–June 19 | 111 | 4.97 | 6.95 |
| Growth period | May 1–June 19 | 50 | 7.62 | 8.04 |
| "Summer" | June 20–Aug. 17 | 59 | 12.11 | 17.97 |
| "Fall" | Aug. 18–Oct. 14 | 57 | 12.31 | 13.64 |
| "Late Fall" | Oct. 15–Dec. 3 | 50 | 9.06 | 6.30 |

TABLE III. *Constants of Frequency Distributions of lengths of Mytilus edulis L. in the St. Andrews Region, New Brunswick. 45 specimens in each experiment*

| Box "A." Level—3 feet above chart datum. | | |
|---|---|---|
| | Beginning of Experiment | End of Experiment |
| Mean | 9.2  ± .06 | 25.2  ± .09 |
| Standard Deviation | .650 ± .046 | .914 ± .065 |

| Box "B." Level—10 feet above chart datum. | | |
|---|---|---|
| Mean | 9.2  ± .06 | 21.3  ± .08 |
| Standard Deviation | .650 ± .046 | .837 ± .059 |

low level occurred during the " spring " season, the absolute increment being 5.1 mm. (percentage addition 55.4). The low water temperatures during March and April (below 5° C.) seem to preclude the possibility of any significant growth taking place during this period. We, therefore, consider the growth period of the " spring " season to extend from about May 1 to June 19.

These results clearly indicate that environmental conditions in the area below the M. L. W. L. are favorable for growth when predatorial action is eliminated, thus supporting the original hypothesis.

The rate of growth obtained at a level of about 10 feet above chart datum was 12.1 mm. (percentage increment 131.5). Very little growth occurred during the " late fall " period, the absolute increment being 1.4 mm. (percentage addition 7.0). The results show a marked reduction as compared with those of Box " A " and corroborate the findings of Mossop ('22); namely, that exposure is accompanied by decrease in growth rate.

## SUMMARY AND CONCLUSIONS

1. The paper constitutes part of the results of an ecological study of the intertidal biota of the region of St. Andrews, N. B., carried on during the period 1929 to 1932.

[4] Seasonal mean water temperatures represent the mean of daily mean temperatures based on the average of two readings taken about 8 A.M. and 5 P.M. Mean air temperatures represent the mean of daily mean temperatures obtained by calculating the mean of the maximum and minimum daily temperatures.

2. Attention has been focused primarily on the *Balanus-Mytilus edulis* Association of the *Balanus-Littorina-Fucus* Biome. The more important community associates of *M. edulis* are listed and certain of the principal interrelationships discussed and defined.

3. The occurrence of true succession in the *Balanus-M. edulis* Association has been demonstrated.

4. The unity of the marine plant-animal community has been discussed and the importance of recognizing plants and animals as inter-related co-acting constituents of an integrated biotic community is stressed.

5. Data are presented to show that starfishes (*A. vulgaris* and *forbesii*) and sea urchins (*S. drobachiensis*) of the subtital *Strongylocentrotus-Asterias Biome,* as well as the whelk (*P. lapillus*) exert a distinct predatorial effect on *M. edulis,* especially at the lower levels. It has also been shown experimentally that this mussel (when sheltered from predators) grows at a normal rate below the M. L. W. L. on areas where mussel communities are totally absent. In other regions of the Bay of Fundy submerged mussel communities occur. Hence it is concluded that the practical absence of mussels below the M. L. W. L. in many areas of the St. Andrews region is due to the above mentioned predators.

6. With regard to the growth of *M. edulis* during 1931, it has been found that (*a*) the length of the growing season extends from about May 1 to December 1 (table II); (*b*) the annual absolute increment of growth for specimens planted at a level of 3 feet above chart datum and possessing an initial length of 9.2 mm. was 16.0 mm. (percentage addition 173.9); (*c*) the corresponding growth at a level of 10 feet above chart datum was 12.1 mm. (percentage addition 131.5). This reduction in growth rate of approximately 25 per cent is due, perhaps, to decrease in amount of available food through increase of exposure; and (*d*) the seasons of greatest growth during 1931 are " spring " and " summer " and a significant amount of growth takes place during the " fall " period (table I).

## Acknowledgments

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# ECOLOGICAL SUCCESSION IN THE *MYTILUS CALIFORNIANUS* HABITAT AS OBSERVED IN MONTEREY BAY, CALIFORNIA [1]

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The study of ecological succession in any area requires an extended period of time during which the selected area may be observed continually. Over a period of two years spent at the Hopkins Marine Station of Stanford University I was afforded an excellent opportunity for observing the succession of plants and animals on a denuded area of the intertidal zone of Monterey Bay.
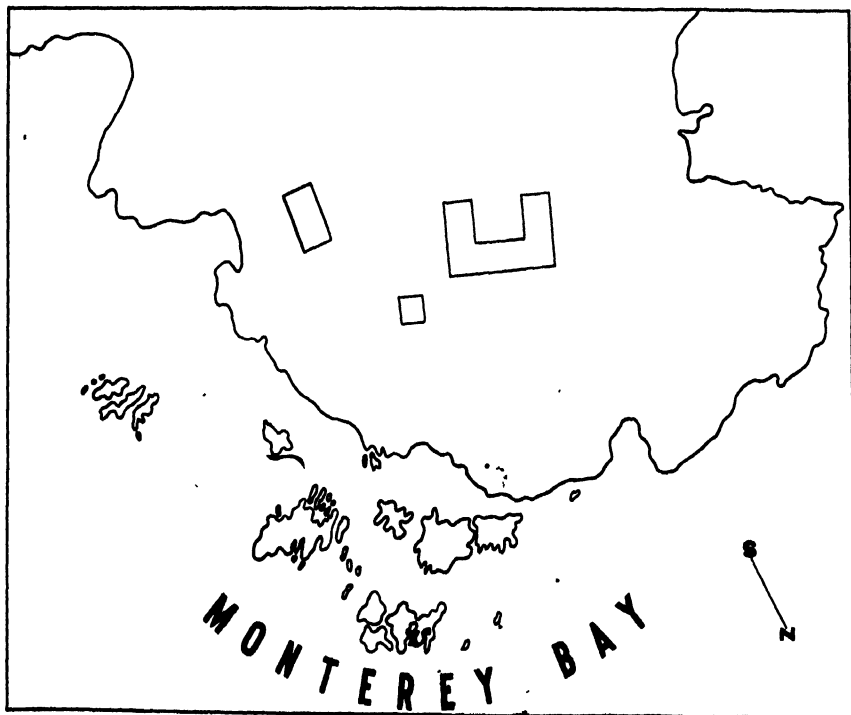


FIG. 1. A map of Cabrillo Point, a promontory on the southern margin of Monterey Bay, on which the Hopkins Marine Station is located. The letter " X " marks the location of the test square.

Fig. 2 a. View of the test square taken in March, 1933.
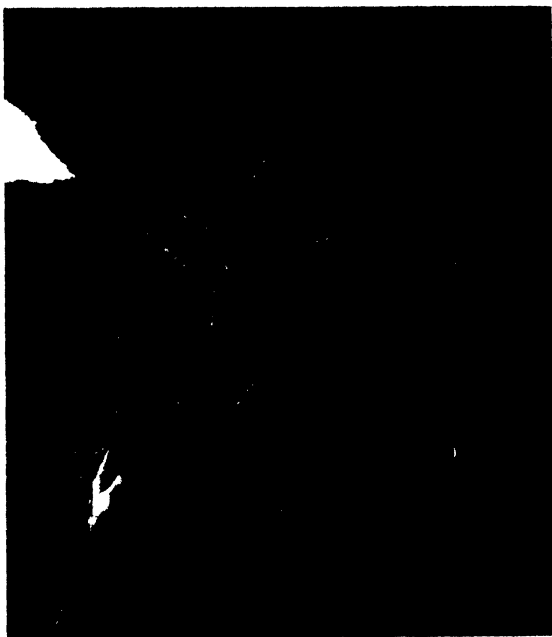
b. View of the test square taken in July, 1934.

The region selected is located on the southern margin of Monterey Bay, California, in the densely populated *Mytilus* beds (fig. 2) of the littoral directly north of the Jacques Loeb Laboratory.

On November 23, 1931, a square yard (fig. 1) in the *Mytilus californianus* habitat was cleared off, scraped, and brushed with a steel brush until no living animals or plants (except microscopic organisms) remained within the area. The space was located on the east side of a vertical rock face. It was protected from the direct force of the waves but was subjected to strong currents of highly oxygenated water. The maximum range of the tides in the region is — 2 feet to 7 feet. The tidal level at the top of the square was 4.8 feet.

The macroscopic contents of the unit area were taken into the laboratory, identified and counted. Table I shows the results of the count. The population apparently represented a climactic biotic condition, a typical *Mytilus californianus* association. In the second column of the table the relative vertical positions of the inhabitants are indicated. The stratification indicated in the table was apparently controlled by the upper margin of the mussel beds which extended along a line about one foot below the top of the square.

It was possible to study the area only at the low tide interval when the sea was relatively calm. At these times many changes in the fauna of the square were noted and counts of the animals were made. The records of these observations are given in tables II, III, IV, V, VI, VII, and VIII.

The barren rock surface soon became covered over by encrusting and film-forming algae. A microscopic examination showed that the green film contained numerous diatoms as well as filaments of algae. The first macro-

TABLE I. *Number of organisms and their distribution found in the test square of the Mytilus beds on November 23, 1931*

| Species | Location | Number |
|---|---|---|
| *Acmaea digitalis* Eschscholtz | upper | 74 |
| *Acmaea persona* Eschscholtz | middle and lower | 114 |
| *Acmaea limatula* Carpenter | upper | 2 |
| *Acmaea scabra* Gould | upper | 128 |
| *Amphipods* (unidentified) | middle and lower | 846 |
| *Amphissa versicolor* Dall | middle and lower | 39 |
| *Balanus glandula* Darwin | upper | 872 |
| *Calliostoma costatum* (Martyn) | lower | 2 |
| *Cirolana harfordi* (Lockington) | middle and lower | 926 |
| *Leptasterias aequalis* (Stimpson) | lower | 6 |
| *Lottia gigantea* Gray | upper and middle | 10 |
| *Mitella polymerus* (Sowerby) | middle and lower | 356 |
| *Mytilus californianus* Conrad | middle and lower | 1612 |
| *Pachygraspus crassipes* Randall | middle and lower | 14 |
| *Petrolisthes cinctipes* (Randall) | middle and lower | 416 |
| *Physcosoma agassizi* Keferstein | middle and lower | 327 |
| *Strongylocentrotus purp.* Stimpson | middle and lower | 19 |
| *Tegula brunnea* (Philippi) | middle and lower | 17 |
| *Tetraclita squam. rub.* Darwin | middle and lower | 78 |
| *Thais emarginata* (Deshayes) | upper and middle | 218 |

scopic animals to inhabit the area were *Lottia gigantea* and three species of *Acmaca, A. digitalis, A. persona,* and *A. scabra.* The numbers of these limpets found on the square after a period of three months are shown in table II.

TABLE II.  *Number of organisms and their distribution found in the test square of the Mytilus beds on February 19, 1932*

| Species | Location | Number |
|---|---|---|
| *Acmaea digitalis* | scattered | 37 |
| *Acmaea persona* | scattered | 18 |
| *Acmaea scabra* | scattered | 6 |
| *Lottia gigantea* | upper | 1 |
| film-forming algae | whole area | abundant |

The month of March apparently marks the beginning of the spawning season of the barnacles. A count of the population of the square area on March 4 revealed the presence of three species of barnacles, *Balanus glandula, Tetraclita squamosa rubescens,* and *Mitella polymerus* (table III).

TABLE III.  *Number of organisms and their distribution found in the test square of the Mytilus beds on March 4, 1932*

| Species | Location | Number |
|---|---|---|
| *Acmaea digitalis* | upper and middle | 173 |
| *Acmaea persona* | lower | 53 |
| *Acmaea scabra* | scattered | 6 |
| *Balanus glandula* | scattered | 95 |
| *Lottia gigantea* | upper | 7 |
| *Mitella polymerus* | lower (14 mm.) | 76 |
| *Tetraclita squam. rub.* | lower | 423 |

Another record was taken on April 25, 1932. The census (table IV) showed a marked increase in the number of *Balanus glandula.* In the lower third of the cleaned area 55 small specimens (4 mm. in length) of *Mytilus californianus* had attached themselves.

TABLE IV.  *Number of organisms and their distribution found in the test square of the Mytilus beds on April 25, 1932*

| Species | Location | Number |
|---|---|---|
| *Acmaea digitalis* | upper and middle | 234 |
| *Acmaea persona* | lower | 72 |
| *Acmaea scabra* | upper and middle | 8 |
| *Balanus glandula* | upper and middle | 2126 |
| *Lottia gigantea* | upper and middle | 8 |
| *Mitella polymerus* | lower (20 mm.) | 109 |
| *Mytilus californianus* | lower (4 mm.) | 55 |
| *Tetraclita squam. rub.* | lower | 416 |
| *Thais emarginata* | lower (large) | 2 |

An examination of the square on June 3, 1932 showed that there was very little change in the population during the month of May (table V).

TABLE V. *Number of organisms and their distribution found in the test square of the Mytilus beds on June 3, 1932*

| Species | Location | Number |
|---------|----------|--------|
| *Acmaea digitalis* | upper and middle | 186 |
| *Acmaea limatula* | middle | 5 |
| *Acmaea persona* | middle and lower | 69 |
| *Acmaea scabra* | upper | 93 |
| *Balanus glandula* | upper and middle | 1967 |
| *Lottia gigantea* | upper and middle | 11 |
| *Mitella polymerus* | lower (24 mm.) | 109 |
| *Mytilus californianus* | lower (11 mm.) | 51 |
| *Nuttallina californica* | scattered (15 mm.) | 2 |
| *Tetraclita squam. rub.* | lower | 378 |
| *Thais emarginata* | scattered (large) | 7 |

An examination of the area on July 18, showed the presence of 367 small specimens of the predaceous whelk, *Thais emarginata* (table VI). Observations that I have recorded on the breeding seasons of the animals in this region indicate that *Thais emarginata* begins depositing egg capsules in March. This fact probably accounts for the abundance of the small whelks at the time this count was made. The average size of the young forms was 5 mm.

TABLE VI. *Number of organisms and their distribution found in the test square of the Mytilus beds on July 18, 1932*

| Species | Location | Number |
|---------|----------|--------|
| *Acmaea digitalis* | upper and middle | 167 |
| *Acmaea limatula* | middle | 4 |
| *Acmaea persona* | middle and lower | 78 |
| *Acmaea scabra* | upper | 82 |
| *Balanus glandula* | upper and middle | 1904 |
| *Lottia gigantea* | upper and middle | 11 |
| *Mitella polymerus* | lower | 109 |
| *Mytilus californianus* | lower | 7 |
| *Nuttallina californica* | lower and middle | 34 |
| *Pachygrapsus crassipes* |  | 4 |
| *Tetraclita squam. rub.* | lower | 371 |
| *Thais emarginata* | lower and middle (5 mm.) | 367 |

At the same time several specimens of *Nuttallina californica* (Reeve) had moved into the cleaned area. No specimens of this chiton were recorded in the previous counts. They were, however, found to be abundant on the outer rocks which are not favorable for the growth of mussels.

The next population count was made in October (table VII). There was a pronounced increase in the number of young limpets. Other records of mine revealed that these limpets began spawning during September. There was, also, a marked decrease in the number of whelks, a condition which was possibly the result of a lack of protection, afforded in the fully developed *Mytilus* association, from strong water currents which sweep the snails from the rocks.

TABLE VII. *Number of organisms and their distribution found in the test square of the Mytilus beds on October 13, 1932*

| Species | Location | Number |
|---|---|---|
| *Acmaea digitalis* | upper and middle (4 mm.) | 323 |
| *Acmaea limatula* | middle | 3 |
| *Acmaea persona* | lower | 150 |
| *Acmaea scabra* | upper and middle (4 mm.) | 521 |
| *Balanus glandula* | upper and middle | 2175 |
| *Lottia gigantea* | upper and middle | 15 |
| *Mitella polymerus* | lower | 109 |
| *Mytilus californianus* | lower | 53 |
| *Nuttallina californica* | lower and middle | 14 |
| *Pachygrapsus crassipes* | lower | 3 |
| *Tetraclita squam. rub.* | lower | 359 |
| *Thais emarginata* | lower and middle | 47 |

Another count made in December revealed no important changes in the population (table VIII).

It has been asserted by some investigators, for example Shelford ('30, p. 219), that there is no ecological succession taking place in the intertidal rock communities. These conclusions were based mainly upon observations on the *Balanus* associations (Pierron and Huang, '26) and marine terrace associations (Wilson, '26). They may be justified in the case of these higher communities where competition for space is not great. My investigations of more crowded intertidal communities, however, have revealed a complete succession of forms.

TABLE VIII. *Number of organisms and their distribution found in the test square of the Mytilus beds on December 26, 1932*

| Species | Location | Number |
|---|---|---|
| *Acmaea digitalis* | upper and middle (6 mm.) | 268 |
| *Acmaea limatula* | middle | 1 |
| *Acmaea persona* | middle and lower | 94 |
| *Acmaea scabra* | upper and middle (6 mm.) | 429 |
| *Balanus glandula* | upper and middle | 2374 |
| *Lottia gigantea* | upper and middle | 15 |
| *Mitella polymerus* | lower | 108 |
| *Mytilus californianus* | lower | 89 |
| *Nuttallina californica* | middle and lower | 9 |
| *Tetraclita squam. rub.* | lower | 329 |
| *Thais emarginata* | middle and lower (12 mm.) | 59 |

According to Shelford ('30, p. 220) there are two main questions to be considered in determining whether or not ecological succession is taking place in a biotic community. They are as follows: (1) Are any of the earlier animals essential to the seating of the later ones? (2) Do forms drop out as the development of the community progresses? Both of these questions can be answered in the affirmative in the case of the exposed mussel beds of the region investigated.

In the biotically climactic condition, the lower two-thirds of the square

yard of surface was covered with *Mytilus californianus* and *Mitella polymerus*. Beneath this layer of mussels and barnacles, a large number of species of animals were found whose existence in this habitat depended upon the protection offered by the sessile forms. For one year after the area was cleaned off, practically none of the shelter-seeking species had returned to the barren rocks.

The records also show that the rock barnacles and the limpets, which in the climactic condition were limited to the upper third of the square, were able to live in a much lower zone in the absence of the mussels. After the heavy growth of barnacles had appeared in the spring, all of the larger limpets were forced to retreat to a higher and less densely inhabited area in order to find sufficient space for attachment and for feeding excursions.　　　•

An additional inspection of the area was made in the summer of 1934, two and one-half years after the square yard was cleaned off. This examination showed that the rehabilitation of the rock surface by the mussels and their associated fauna was far from complete. An area approximately 18 inches square, located on the lower two-thirds of the test square was covered by *Mytilus* and *Mitella*. It was noted that in addition to the relatively independent development of the association near the center, there was an encroachment upon the cleaned area by the surrounding *Mytilus* association. No quantitative data were taken at this time (fig. 2*b*).

The results of this investigation seem to indicate that ecological succession in the *Mytilus* habitat progresses in the following manner: (1) a clean area first becomes covered with a film of algae; (2) those forms which feed on this algae growth, such as the limpets, are the first animals to appear in the area; (3) during their respective spawning seasons the mussels, goose barnacles and rock barnacles attach themselves to the cleaned surface; (4) these sessile forms gradually come to occupy the greater part of the surface and make the habitat unfavorable for the larger specimens of limpets; (5) the limpets thus move to a higher zone in which the mussels and barnacles cannot exist. The upward migration of the limpets becomes quite evident soon after the appearance of the rock barnacles. The concentration of the larger limpets along the upper margin of the *Balanus* covered area forms a very obvious line.　　　•

A comparison of the records given in table 1 with those of table VIII indicates that *Balanus glandula* is not able to survive beneath the layer of mussels, but another rock barnacle, *Tetraclita squamosa rubescens*, is found in appreciable numbers under the growth of these mussels. A similar condition was found to obtain on that part of the foreshore protected from wave action. *Tetraclita squamosa rubescens* was abundant beneath the heavy growth of *Fucus* and *Pelvetia,* but the lower range of *Balanus glandula* ended abruptly at the top of the plant habitat. This variation in the distribution of these two barnacles may be caused by structural differences in the shells. The aperture of the shell of *Tetraclita* is small and the movements of the

cirri are not disturbed by overhanging growths of sea weeds or mussels. The shell of *Balanus,* on the other hand, is relatively open and any disturbance of the cirri causes their immediate retraction.

It should also be noticed that *Mytilus californianus* has a distinctly limited distribution within the littoral of the region investigated. The fact that the reoccupation of the cleaned area by the mussels was promptly begun, while at the same time no perceptible spreading into new areas took place, clearly demonstrates that the general distribution of this species is not random in nature. It is, on the contrary, strictly regulated by environmental factors.

## CONCLUSIONS

1. Ecological succession is taking place in the densely populated *Mytilus californianus* habitat. It is shown that some of the earliest inhabitants are essential to the seating of some of the later animals and that certain species drop out during the development of the climactic condition.

2. A full reestablishment of a climactic condition requires quite a long period of time (at least more than two and one-half years). This fact, in addition to its ecological significance, also has a practical bearing. It demonstrates the caution which should be exercised in the commercial exploitation of the *Mytilus* beds.

3. The rock barnacle, *Tetraclita squamosa rubescens,* can exist beneath the mussel beds while *Balanus glandula* does not live under similar conditions.

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# ORIGIN OF WHITE PINE IN VIRGIN FOREST STANDS OF NORTHWESTERN PENNSYLVANIA AS INDICATED BY STEM AND BASAL BRANCH FEATURES

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It is common knowledge that white pine, *Pinus strobus* L., was an important component of the primeval forests in northwestern Pennsylvania. It appears that the species generally occurred as scattered individuals in mixture with hemlock and hardwoods but occasionally formed pure or nearly pure stands. In view of the inability of white pine to satisfactorily reproduce and develop under dense canopies of species such as hemlock, beech and sugar maple, the question naturally arises as to how it originated in the virgin stands. Did the virgin white pine originate on relatively open forest sites, as pure pine stands commonly do today, or did it develop under relatively open forest canopies? Heretofore, so far as is known to the writers, there has been no direct attempt to answer this question.

The methods employed in the investigation here reported consisted essentially in comparing stem and basal branch features of pines which developed in virgin forest stands with the features of pines now developing (1) on open sites such as clear cut or old field areas and (2) on sites which support a somewhat open forest stand (density usually 0.3 to 0.6, which appears to be about the maximum density under which white pine is capable of development). All trees employed in the study developed on similar welldrained soils in the same general climatic region.

Data representing virgin forest conditions were obtained from two localities in northwestern Pennsylvania, namely, Heart's Content and Ludlow. At Heart's Content the pine occurred as scattered individuals in a virgin hemlock-beech stand. Based on the number of individuals in the dominant tree class white pine had an abundance of approximately 11 per cent; there were about 7 pine trees per acre. At Ludlow the virgin stand contained a considerably larger proportion of pine; in fact it must have approached a pure pine forest over portions of the area. The average number of pine trees per acre was about 20. From the standpoint of size the pines in these two virgin stands were similar.

## STEM GROWTH

Stem growth at stump height (approximately 75 cm.) was determined for pine trees in the Heart's Content stand, for trees in stands which developed on open sites and for trees which developed under partial canopies. Growth during the first decade was measured on two radii and averaged for each tree. The summarized data are presented in table I and figure 1. Owing to the decadent character of the stumps it was impossible to obtain corresponding data for the Ludlow locality.

TABLE I. *Stem and branch features of white pine which developed under various conditions*

| | Condition | | | |
|---|---|---|---|---|
| | Virgin (Heart's Content) | Virgin (Ludlow) | Open site | Partial forest canopy |
| *Stem growth* | | | | |
| Number of stems | 59 | | 20 | 43 |
| Mean radial growth, first decade, cm. | 1.39 | | 4.05 | 1.22 |
| *Branch age* | | | | |
| Number of branches | 24 | 34 | 23 | 17 |
| Mean age, years | 16 | 15 | 14 | 13 |
| *Branch size* | | | | |
| Number of branches | 25 | 52 | 23 | 17 |
| Mean diameter, cm. | 0.89 | 2.18 | 2.41 | 0.92 |
| *Branch growth* | | | | |
| Number of branches | 23 | 34 | 23 | 17 |
| Mean radial growth, first decade, cm. | 0.36 | 0.83 | 1.05 | 0.43 |

With reference to mean radial growth during the first decade (age at stump height, not corrected to total age) there is a significant difference [1] between the trees which developed on open sites and those which developed in the virgin forest at Heart's Content; on the other hand, trees which developed under partial canopies and those which developed at Heart's Content are similar. Even in the absence of other evidence (see below), these facts might well be interpreted as indicating that the Heart's Content pine originated under a partial canopy, that is, under a canopy density of about 0.3–0.6. It is clear that these pines did not develop on a bare or open site and it seems equally certain that they could not have developed under a full canopy.

Basal branches were obtained from stumps of trees which developed under the following conditions: (1) virgin forest (Heart's Content), (2) virgin forest (Ludlow), (3) open or bare sites, and (4) under partial forest canopies. All branches were obtained at a point approximately 75 cm. above

[1] The significance of the difference between means was tested statistically using the "t" test of Fisher (1932) and Tippett (1931).

A
1.39 cm.

D
1.22 cm.

A
0.36 cm.

D
0.43 cm.

B
0.83 cm.

C
1.05 cm.

Branch growth, first decade

C
4.05 cm.

A
0.44 cm.

D
0.46 cm.

B
1.09 cm.

C
1.20 cm.

Stem growth, first decade      Branch size
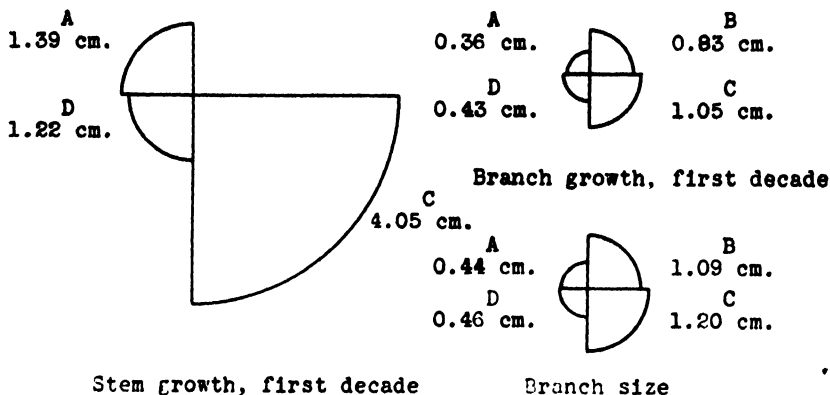
FIG. 1. Stem and branch features of white pine which originated in virgin stands at Heart's Content (A), Ludlow (B), on open areas (C), and under partial forest canopies (D). Mean radial dimensions in cm.

## BASAL BRANCH FEATURES

ground level and measurements were made at a point about 15 cm. out from the center of the stem. In every case the branches were dead. The data are presented in table I and figure 1.

Branch ages were investigated but no important differences could be established, even between trees which developed on open sites and trees which



FIG. 2. A decadent white pine stump in the Ludlow area with a whorl of six large branch stubs about 60 cm. above the ground. The branch stubs are in place and average about 3.5 cm. in diameter. The tree evidently originated on an open site.

developed under partial forest canopies. Therefore, it appears that no inference regarding the conditions under which the white pine originated can be drawn from this feature.

On the other hand, diameters of basal branches from trees now developing under partial canopies are significantly different from those of trees on open sites. Branches from trees at Heart's Content agree with the former and branches from trees at Ludlow agree with the latter. This indicates that the Heart's Content pine originated under a partial forest canopy and that the Ludlow pine originated on a practically open site. Figure 2 illustrates the large size of the basal branches in the Ludlow trees.

With respect to mean radial growth (first decade) of basal branches the virgin pine at Heart's Content shows essentially the same features as branches of trees now developing under partial forest canopies. This agreement is in accord with the data relating to both stem growth and branch diameter. The radial growth of basal branches from the virgin pine at Ludlow, on the other hand, parallels that of branches from trees which originated on open sites.

## DISCUSSION

The early stem growth and the branch development (size and rate of growth) of white pine originating on open sites and under partial canopies is significantly different. By comparison of these features in virgin pine trees and in trees originating under known conditions it is indicated that the Heart's Content pine originated under a partial forest canopy rather than on an open site. This interpretation is in agreement with the known facts concerning this virgin stand and the silvical habits of white pine. In 1930 the senior author expressed the view that the pine at Heart's Content was essentially even-aged, and later Hough ('32) reached the same conclusion. Additional data on ages have cast doubt upon this idea; it now appears that the pine is not even-aged in the ordinarily accepted sense of the term. It should be kept in mind that although the Heart's Content pine is uneven-aged it is by no means all-aged; age classes below about 175 years are not represented. As has been pointed out in this report the proportion of white pine at Heart's Content is relatively low, only about 7 trees per acre. The available evidence indicates that these scattered trees originated under a partial forest canopy and there appears to be no reason for holding a contrary view.

The virgin pine at Ludlow evidently originated on an open or nearly open site. This is indicated by the large size of the basal branches, an example being shown in figure 2. With respect to both size and rate of growth basal branches from the pine at Ludlow are significantly different from the branches of pine which originated under partial forest canopies and in the virgin stand at Heart's Content.

The idea that the virgin pine at Heart's Content and at Ludlow originated under different site conditions is in no sense contradictory. In the Heart's Content stand the proportion of pine was low, whereas in the Ludlow stand it

was much higher. It is generally accepted as a fact that throughout the eastern part of its range, at least, pure or nearly pure white pine stands usually originated on relatively open sites. Such stands are approximately even-aged. It is also a fact that under the unbroken canopy of fully stocked climax stands of hemlock and hardwoods white pine is unable to reproduce satisfactorily. Within these two extremes the proportion of white pine and its age characteristics will ordinarily vary according to the density of the crown cover.

On open sites white pine tends to develop into pure or nearly pure stands which are essentially even-aged. Under canopies only occasional white pines become established from time to time as openings are made by the death of trees. Hemlock and many hardwoods, being more tolerant, come in more regularly and in greater numbers. When this reproduction develops and the stand matures the proportion of white pine is relatively low and the spread of ages is large compared with stands which originated on open sites. It is probably also true that the proportion of white pine tends to be higher on the lighter soil types than on heavier ones.

It appears that ecologists have not generally recognized the possibility of using stem and basal branch features in connection with investigations of the past history of forest stands. The authors believe that features such as those employed in the investigation set forth above often may furnish a reliable index of past conditions which would otherwise be difficult if not impossible to secure. In this connection attention may be called to the recent work of Griggs ('34) in which features such as rate of stem growth, tree age and basal branch size were used effectively in studies of the forest front in southwestern Alaska.

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# COORDINATE METHOD OF MAPPING LOW SHRUBS [1]

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A large number of plots selected at random to eliminate the personal factor in plot selection and to assure obtaining data that are representative of the area being studied are now recognized as essential in studying plant populations. Although one or two carefully selected plots representing average conditions on an area several hundred times the size of the plot will afford some measure of conditions, a larger number of smaller sized plots selected at random will give much more reliable data. The larger number of plots also is better suited to statistical analysis and necessitates a rapid and reasonably accurate system of mapping and summarizing the data. To meet this need in the study of shrubby vegetation, a method of charting the location and perimeter of crowns of low shrubs has been developed in connection with investigations made on sagebrush-wheatgrass and desert shrub ranges by the Intermountain Forest and Range Experiment Station. This new manner of charting, termed the " coordinate method " has many distinct advantages over methods previously used and may be useful in mapping the undercover on silvicultural plots as well as in range studies.

One common method of approximating the quantity of shrub cover on sample plots is to estimate occularly the shrub densities as is done in range surveys.[3] Another more accurate method is actually to map the crown spread of the shrubs on the plots. Both methods, as previously used, have serious deficiencies.

The system of recurrent occular estimates serves to detect major invasion or retrogression of any particular species. However, since it deals only with average quantities and since no map is made, it does not provide a detailed picture of the distribution of plant species on the plot nor of changes that have occurred between mappings. Furthermore the data on average quantities obtained are not sufficiently accurate for many purposes.

For critical study, it is necessary accurately to map the location and crown

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[1] Acknowledgment is made to Selar S. Hutchings and J. F. Pechanec, Junior Range Examiners, Intermountain Forest and Range Experiment Station for valuable assistance in developing the technique of the coordinate method.

[2] Assistant Silviculturist and Senior Forest Ecologist respectively, Intermountain Forest and Range Experiment Station, Ogden, Utah.

[3] For detailed information on this method, see Instructions for Grazing Reconnaissance on the National Forests, 1927, which may be obtained from the Forest Service, U. S. Department of Agriculture, Washington, D. C.

spread of shrub species on a series of permanently established plots to deter-
mine how, under what conditions, and in what degree invasion or retrogres-
sion of these shrub species is taking place.    Two common methods of map-
ping shrubs are with the planetable and with the gridiron system as described
by Nelson.[4]    These methods are commonly used on square plots 16.5 or 33
feet on a side.

    The first-named method consists of setting up a planetable within the
plot and with the aid of a small alidade, a surveying tape and a flagpole, sight-
ing in and locating sufficient points on the perimeter of each bush to enable
the mapper to sketch in the crown spreads on the map sheet.    While this
method is perhaps the most feasible for mapping tall shrubs such as oakbrush,
it is at best a slow and tedious process for low shrubs.    It requires two men,
one to map and the other to hold the tape and the flag.    Setting up and
orienting the table is time-consuming.    There is considerable chance for error
in the many measurements required to spot in the perimeter of a shrub.    A
major fault is that the mapper cannot critically observe the shrub he is sketch-
ing in order to map in the details of crowns with irregular spreads, without
frequently leaving the planetable and walking over to examine the shrub.

    In the gridiron system the plot is subdivided with cord into squares of a
convenient size, usually one or two feet on a side, and the shrubs and the
perimeter of the crowns mapped in by measuring out from the intersections
of the cord and locating the points directly on a map sheet made from ordi-
nary coordinate paper of a suitable scale.    This method allows the mapper to
see each plant in detail as the mapping progresses, thereby aiding materially
in sketching.    However, mapping the larger square plots by the gridiron
method is slow and tedious both in placing the cord preparatory to mapping
and in the actual mapping.

## THE COORDINATE METHOD

    The coordinate method of mapping shrubs is a modification of the gridiron
method, involving the use of special equipment and procedure for speeding up
the operation without a sacrifice of accuracy.    The equipment as shown in
figure 1, is simple.    It consists of four steel rods or stakes ⅜-inch in diam-
eter from 3 to 5 feet in length, depending on the height of the shrubs to be
mapped, sharpened at one end and fitted with an adjustable steel clamp; two
flat steel surveying tapes graduated in feet and tenths of feet and a light metal
cross bar slightly more than 4 feet long, graduated in feet and fifths of a foot.

    The adjustable clamp on each rod is so constructed that it may be set at
any desired height on the rod.    For convenience in adjusting the clamps,
marks are cut in each rod at intervals of one inch.    The clamp is slotted at
right angles to the length of the rod to receive the surveying tape and is fitted
with a thumbscrew to fasten the tape securely.

    [4] Nelson, E. W.    1930.    Methods of studying shrubby plants in relation to grazing.
*Ecology* 11: 764–769.

The metal crossbar is made of duraluminum or other suitable light but strong material. For mapping plots, or segments of plots 4 feet in width, the crossbar is 4 feet and 2 inches in length. It is of T-beam design and made of $\frac{3}{16}$-inch gauge metal with a $\frac{3}{4}$-inch flange and a $\frac{1}{2}$-inch stem. Two notches $\frac{1}{2}$-inch in depth and just wide enough to accommodate the width of the steel
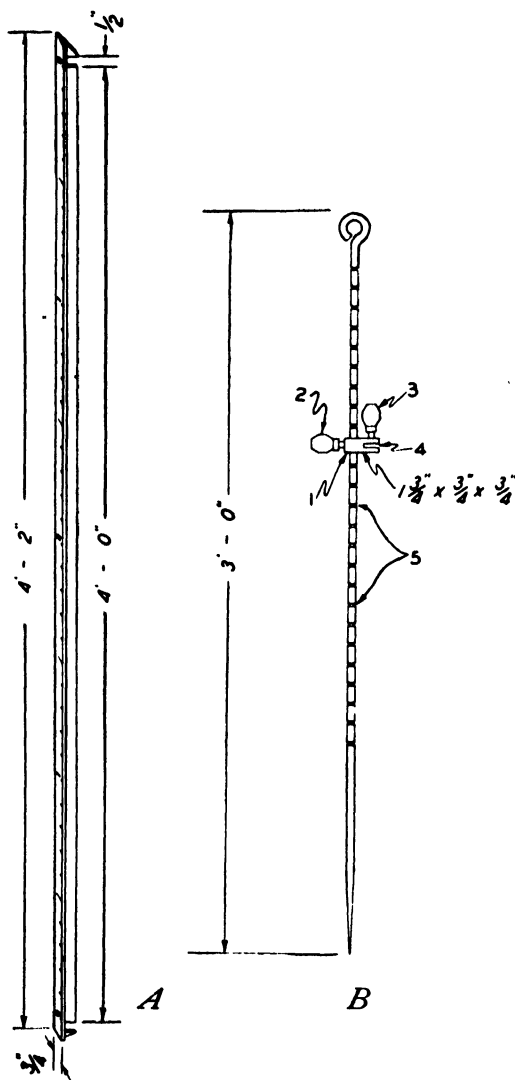


FIG. 1. Equipment for the coordinate method. *A*. Light metal crossbar graduated in feet and fifths of a foot. *B*. Stake and clamp; 1, adjustable steel clamp to hold surveying tape; 2, thumbscrew to hold clamp; 3, flat-nosed thumbscrew to secure surveying tape; 4, horizontal opening in clamp to receive surveying tape; and 5, graduations on stake at 1 inch intervals for adjusting height of clamps.

tape, are cut in the stem to hold the crossbar in position. The distance between the inside edges of the notches is exactly 4 feet. The flange is plainly and legibly graduated in feet and fifths of a foot.

In setting up the equipment, on a plot 4 by 25 feet in size, as shown in figure 2, the sharpened steel rods are pushed or driven into the ground at each



Fig. 2. Mapping sagebrush by the coordinate method.

corner of the plot and the clamps are adjusted to the desired height. The end of each of the two steel tapes is fastened in the clamp on each of one pair of end stakes. Each tape is then stretched along one side of the plot and secured in the clamp on the stake at the farther corner. The tapes should be stretched sufficiently taut to support the 4-foot crossbar without much sagging when the bar is laid across the tapes at right angles to them. With the crossbar in place mapping is ready to begin.

Only one man is needed to do the mapping. The crossbar is first placed at the zero end of the parallel tapes. The mapper, looking perpendicularly down at the shrubs, observes each point where the edges of each individual crown intersect the crossbar and then plots the point on cross-section paper on which the boundaries of the plot have been previously drawn to scale. Having established these points at the first position the crossbar is advanced to the 0.5 foot mark on the parallel tapes, and all points of intersection at the second

position are plotted. The segments of perimeters of each crown between these located points may be sketched in readily. The crossbar is advanced progressively from one end of the plot to the other until the location and crown perimeters of all the shrubs occurring on the plot have been mapped in. Almost any reasonable amount of detail in charting may be secured. If it is desired to record the height of each shrub this measurement may be made as each shrub is charted, and the data entered in small figures within the perimeter of the crown on the map. One experienced man can map six plots per day with this method in dense sagebrush, using a sketching interval of 0.5 feet and a plot area of 4 by 25 feet.

The coordinate method and equipment as described herein is especially adapted for plots or segments of plots, 4 feet wide and 25 feet long. This size of plot has proved highly satisfactory in mapping sagebrush and other low shrubs since it lends itself readily to rapid mapping and compilation. A plot containing one hundred square feet or multiples thereof, has an advantage in that areas of crown spread, expressed in square feet, may be converted directly into percentage of the total area of the plot. The use of a crossbar longer than 4 or 5 feet is not recommended since the additional weight causes excessive sagging of the tapes. Plots or segments more than 25 feet in length may be mapped by using longer tapes and an additional pair of supporting rods and clamps placed midway between the end rods.

# REVIEWS

## Phytogeography of the Yucatan Peninsula [1]

All who are interested in the study of Mayan civilization will welcome this contribution to the vegetation of the Yucatan Peninsula. An idea of the scope of the work may be gained from the subjects treated. These include physiography, climate, soils, destructive influences, local ecological nomenclature, formations and associations, phytogeographical divisions, summary, list of species in Campeche. The survey is based on data gathered during four growing seasons in Yucatan, Campeche, and the northern portions of Guatemala and British Honduras.

The northern part of the peninsula is remarkable in being very flat and almost entirely devoid of surface streams, whereas the southern portion is rolling or hilly with some streams and lakes and many wooded swamps. The northern half of the peninsula is characterized by low rainfall (17.82 inches at Progreso) although quite humid and cloudy. Southward the rainfall increases in amount and reaches an annual average of 60 to 80 inches in Northern Guatemala.

The vegetation types are closely correlated with the above physical conditions. The northern section supports only a secondary scrub, the plateau in Campeche a dry forest, and the southern portion in Guatemala a great rain forest. In his description Lundell has made clever use of the land and vegetation classification of the natives which is " so serviceable and natural that it needs only to be taken over and scientifically formulated in order to make available to science information what is already folk knowledge." This folk classification takes into consideration physiography, succession and dominance in each area. For instance *akalché* is Mayan for a wooded swamp; where the dominant plant is *palo de tinta*, the area is called a *tintal*, since the addition of the suffix *-al* is used to designate an association. In his outline the author includes both primary and secondary successions in the coastal formations and in both the coniferous and broad-leaved forest climaxes.

The reader will undoubtedly be surprised at the great number of plants, especially of hydrophytes and halophytes, which are established also in the southern United States. It is to be regretted that more has not been accomplished in the study of salt marshes because of the present interest in these areas and especially since " in the few collections made by the writer, the percentage of novelties was remarkably high." The trained ecologist may not agree with the usage of the terms ' formation ' and ' association ' as used by

[1] Lundell, Cyrus L. 1934. Preliminary Sketch of the Phytogeography of the Yucatan Peninsula. Carnegie Inst. Wash. Publ. 346: 253–325.

the writer. Many would wish for a more complete delineation of the plant communities but, as the writer points out, this can be accomplished only by years of study. In spite of unavoidable omissions this preliminary sketch (as it is modestly titled) of the phytogeography of this region should be an easily available reference work for every botanically-minded student of Middle America.

<div align="right">WM. T. PENFOUND</div>

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## MOSS FLORA OF NORTH AMERICA

Plant associations in all except the semi-arid and arid places of the earth are more or less composed of mosses and liverworts. And yet in most literature these interesting and suggestive plants are either omitted or very inadequately treated. This is due largely to our lack of suitable manuals for determining the species. For liverworts we have the thalloid forms in Flora of North America. The same series has covered the lower Musci, but without illustrations. It is peculiarly fortunate therefore that Dr. A. J. Grout, as All-year Member of the Staff of the Biological Laboratory at Cold Spring Harbor, is publishing a rather sumptuous monograph of the Moss Flora of North America.[1] This will make a knowledge of mosses available to anyone who has some patience, and a microscope.

Volume III of the Moss Flora (the only volume yet completed) was begun in 1928 and finished in August 1934. The volume has 277 pages and 80 plates, and covers the Musci Pleurocarpi. With this and Dr. Grout's Mosses with hand lens and microscope one can have a diagnostic figure of practically every pleurocarpous moss species on this continent north of Mexico, including Alaska and Greenland. Wherever possible the figures are copies of classic drawings. Where these were inadequate new pictures have been made. This is particularly true in Fontinalaceae, by Dr. Winona H. Welch.

In November 1933 the Grimmiaceae by George N. Jones was published as part 1 of Volume II. Other parts of this volume are in preparation, and will appear from time to time. The completion of this work will certainly contribute to the enrichment of our writings and collections, and to the joys of botanizing, alike for the amateur and for the professional botanist.

<div align="right">H. S. CONARD</div>

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[1] Grout, A. J. Moss Flora of North America North of Mexico. **2** (1): (Grimmiaceae, by Geo. Neville Jones), pp. 1–66, pl. 1–25, 1933. **3**: (Pleurocarpi), pp. 1–278, pl. 1–80, 1928–1934. *Publ. by A. J. Grout, Newfane, Vt.*

## Living Plant Materials in Prairie Soils [1]

Experiments have shown that grass land is the most effective herbaceous cover for controlling run-off and erosion. The reason for this is shown in a recent publication by Dr. J. E. Weaver and Geo. W. Harmon, on the amount of living plant material in the different kinds of soil for the most common types of grass and pasture land in eastern Nebraska. The study showed the lowland prairie, of which big bluestem, *Andropogon furcatus,* is the dominant species, to have the largest volume and dry weight of the underground plant parts of any of the grasslands analyzed. This averaged 4.1 tons per acre for the top four inches of soil and 1.3 tons for the soil layer located between 4 and 12 inches. The volume occupied by this material averaged 378 cubic feet per acre for the top four inches and 132 cubic feet for 4 to 12 inch soil layer. Little bluestem, *Andropogon scoparius,* the dominant grass in the natural upland prairie ranked second in yield of underground parts. Blue grama, *Bouteloua gracilis,* and buffalo grass, *Bulbilis dactyloides,* which invade the prairie as a result of overgrazing ranked third and fourth in the order named in amount of root material in the soil. *Stipa spartea,* which grows in the drier habitats of the upland prairie, ranked last of the native grasses that were studied in quantity of underground parts. Bluegrass, *Poa pratensis,* which replaces the bluestem grasses as a result of overgrazing had less underground living parts than either big or little bluestem. The analysis of the underground parts from different kinds of pasture showed that the quantity of this material was very materially reduced by overgrazing, the amount being about 70 per cent less in the final stage of degeneration for the little bluestem type and about 72 per cent for the big bluestem type.

All the native sod was very resistant to washing, the resistance being greatly reduced by overgrazing. The large amount of root material was shown to effectively bind and hold the soil in place which is responsible for the resistance of grassland to erosion. Methods were devised for determining the root content of the different types of grassland and for measuring the resistance to washing. These are clearly described in the bulletin. The publication also discusses plant cover in relation to rainfall interception, decrease in run-off and promotion of absorption, and the underground parts in relation to pore space, soil structure and erosion. This publication should be especially valuable to all plant ecologists and to agriculturalists interested in the problem of run-off and erosion.

A. E. Aldous

Kansas State College of Agriculture,
Manhattan, Kansas

[1] J. E. Weaver and George W. Harmon. 1935. Quantity of Living Plant Materials in Prairie Soils in Relation to Run-off and Soil Erosion. *Conserv. and Soil Survey Div., Univ. Neb., Bull. B.*

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# PROCEEDINGS

## BUSINESS MEETINGS OF THE ECOLOGICAL SOCIETY OF AMERICA AT PITTSBURGH, PENNSYLVANIA, DECEMBER 27 AND 28, 1934

### Meeting of December 27, 1934

The Society met at 9:45 A.M., with President Fuller presiding.

The President announced the previous appointment of a committee to prepare a special or Festschrift number of ECOLOGY in honor of Professor Emeritus Henry Chandler Cowles. The committee consisted of William S. Cooper (Chairman), Charles C. Adams, Helen Dixon, George D. Fuller, and G. E. Nichols.

President Fuller then appointed new committees as follows: Nominating Committee: E. B. Powers (Chairman), George E. Nichols, and A. O. Weese. Auditing Committee: M. S. Markle (Chairman), Orlando Park, and Lewis M. Turner. Committee on Resolutions: Francis Ramaley (Chairman), E. Lucy Braun, Henry J. Oosting.

The Secretary announced the result of the mail ballot on the proposal to amend Article 4 of the Constitution, the purpose of the amendment being to give greater continuity to the affairs of the Society. Of the votes received up to December 24, 100 were in favor of the amendment, 4 were against. The amendment was declared carried. The amended sentences of Article 4 now read:

" These officers [president, vice-president, and secretary-treasurer] with the past presidents of the two years immediately preceding (as ex-officio members), shall constitute the Board of Directors [1] of the Society. Upon the retirement of a secretary-treasurer, he too shall be an ex-officio member of the Board, for the term of one year."

At the Ecologists' Dinner, Thursday evening at the University Club, Dr. Cooper reported in some detail the favorable progress of the work of his committee in obtaining subscriptions toward the cost of the Cowles' Festschrift number of ECOLOGY, which will be the July, 1935 issue; and he indicated some of the invitation articles which will be included. The assembled company paid tribute to Professor Cowles by a rising vote expressing unanimous approval of this project. President Fuller transmitted to Professor Cowles a letter of appreciation from the Society.

At a meeting of the Executive Committee later in the evening of Decem-

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[1] The designation Board of Directors is the one used in the articles of incorporation of the Society, but this body is more frequently referred to as the Executive Committee, as it was formerly called officially.

ber 27, it was decided that a statement of facts relative to the former Secretary-Treasurer, Dr. Kienholz, be prepared, that this statement be transmitted to Dr. Kienholz allowing him time to reply and make any necessary corrections, and that the statement so revised be published in ECOLOGY as a part of the proceedings. The statement is as follows:

### STATEMENT CONCERNING THE FORMER SECRETARY-TREASURER

The Proceedings published in the April, 1934 number of ECOLOGY contained no financial report from the retiring Secretary-Treasurer, Dr. Raymond Kienholz, but mentioned the reasons which prompted his resignation, which were the lack of an academic connection and of the time necessary to devote to secretarial work. The pressure of his duties during much of 1933 and since have prevented the preparation by him of a financial report for the fiscal year ending November 30, 1933, and of his part in the transactions of the next year. Presumably there are other records of the Society's affairs during 1932 and 1933 of which the officers are still in ignorance. The treasurer's report for 1934 includes items disbursed by Dr. Kienholz after November 30, 1933, one of which is a cash balance transmitted to his successor. Membership records, addressograph plates, copies of the Bulletin of former years, securities representing the Society's investments of the life membership fund, etc., were forwarded to the secretary's office early in 1934. A record book containing the financial history of the Society, and possibly other records, have not as yet been turned over. Dr. Kienholz has not stated when, or whether, this book and his financial report will be forthcoming.

(Signed) GEORGE D. FULLER, *President,*
PAUL S. WELCH, *Vice-President,*
A. G. VESTAL, *Secretary-Treasurer.*

### Meeting of December 28, 1934

The final business meeting followed the Friday afternoon joint session with the Society of American Foresters.

The meeting was called to order at 4:45 P.M. with President Fuller in the chair.

### REPORT OF THE SECRETARY-TREASURER
### December 1, 1933 to November 30, 1934

#### RECEIPTS AND DISBURSEMENTS

*Received by Raymond Kienholz* ........................................
*Disbursed by Raymond Kienholz:*
    Printing, December Bulletin ...............................
    Postage .................................................
    Expenditures incident to Boston Meeting ...................
    ECOLOGY payments for members .......................... $ 402.00
    Ecological Monographs, payments for members ............. 35.00
    Committee on Preservation of Natural Conditions ........... 32.30
    Cash balance turned over to A. G. Vestal ................... 44.43

*Received by A. G. Vestal:*

|  |  |  |
|---|---|---|
| Dues from members, for 1933 .............. | $   42.00 | |
| Dues from members, for 1934 .............. | 1,724.70 | |
| Dues from members, for 1935 .............. | 441.50 | $2,208.20 |
| Interest on apartment-house bonds ......................... | | 62.00 |
| Proceeds, Investors Trustee Shares ........................ | | 48.53 |
| Contributions for Preservation Committee .................. | | 10.00 |
| Royalty, Naturalists Guide ................................ | | 3.50 |
| Sale, August Bulletin ..................................... | | 2.00 |
| Balance from Raymond Kienholz .......................... | | 44.43 |

Total receipts ....................................... $2,378.66

*Disbursed by A. G. Vestal:*

|  |  |
|---|---|
| ECOLOGY, payments for members .......................... | $1,073.00 |
| Ecological Monographs, payments for members ............. | 270.00 |
| Printing, Bulletin (Mar., June, Aug., Oct. nos.) ............. | 142.58 |
| Other printing .......................................... | 89.13 |
| Equipment ............................................. | 3.46 |
| Addressograph plates and work ........................... | 6.31 |
| Multigraphing and addressing new-member letters ........... | 20.00 |
| Clerical work .......................................... | 30.38 |
| Preservation committee .................................. | 51.71 |
| Postage ............................................... | 81.79 |
| Mailing permit 71, third class, Urbana P.O. ................. | 10.00 |
| Express and telegrams ................................... | 7.81 |
| Check tax and exchange charges .......................... | 2.25 |
| Refund of dues ......................................... | 5.00 |

Total disbursements ...................................$1,793.42

Balance on hand ............................................... 585.24

$2,378.66

## ASSETS AND LIABILITIES AS OF NOVEMBER 30, 1934

*Assets*

|  |  |
|---|---|
| Cash on hand .......................................... | $ 585.24 |
| Accounts receivable, interest ............................ | 14.00 |
| Bonds (face value $900.00), estimated value ............... | 540.00 |

Total assets .......................................... $1,139.24

*Liabilities: Bills payable*

|  |  |
|---|---|
| ECOLOGY (1935 payments for members) .................. | $ 252.00 |
| Ecological Monographs (1935 payments) .................. | 75.00 |

Total liabilities ....................................... $ 327.00

Net assets ............................................ 812.24

$1,139.24

## REPORT OF THE AUDITING COMMITTEE

We have examined the Treasurer's financial report for 1934 and believe it to be a correct statement of the Society's financial transactions.

> (Signed) M. S. MARKLE
> ORLANDO PARK
> LEWIS M. TURNER

The reports of the Auditing Committee and of the Secretary-Treasurer were received and upon motion duly seconded were approved.

## MEMBERSHIP REPORT, 1932–1934

The following data show that the decline in membership experienced during the past few years by most scientific societies, has for the Ecological Society been checked (at least for the present). Memberships appear to be slightly on the increase. Sustaining memberships and subscriptions to ECO-LOGICAL MONOGRAPHS are, however, fewer than before. The value of ECOLOGICAL MONOGRAPHS and the need for its continuance with much more nearly adequate support are shown by the continued receipt of manuscripts in much greater quantity than can be published. Additional sustaining memberships and subscriptions to ECOLOGICAL MONOGRAPHS are urgently needed.

In the following tables, *As* refers to associate members; *A* to active; *I*, institutional, *S*, sustaining, *SI*, sustaining instutional; and *L*, life members of three classes, whose numbers, remaining constant for the period covered, are: life members 7, sustaining life 2, life and sustaining 2.

### PAID-UP MEMBERSHIPS

|  | *As* | *A* | *I* | *S* | *SI* | *L* | *Total* |
|---|---|---|---|---|---|---|---|
| 1931 | 26 | 455 | 3 | 93 | 4 | 11 | 592 |
| 1932 | 34 | 432 | 6 | 68 | 3 | 11 | 554 |
| 1933 | 26 | 385 | 6 | 71 | 3 | 11 | 502 |
| 1934 | 28 | 396 | 5 | 65 | 2 | 11 | 507 |

### TOTAL MEMBERSHIP ROLL

|  | *As* | *A* | *I* | *S* | *SI* | *L* | *Total* |
|---|---|---|---|---|---|---|---|
| 1931 |  |  |  |  |  |  | 639 |
| 1932 | 39 | 483 | 6 | 71 | 3 | 11 | 613 |
| 1933 | 31 | 431 | 6 | 74 | 4 | 11 | 557 |
| 1934 | 32 | 435 | 6 | 69 | 3 | 11 | 556 |

### MEMBERS ONE YEAR IN ARREARS

| At end of | *As* | *A* | *I* | *S* | *SI* | *Total* |
|---|---|---|---|---|---|---|
| 1932 | 5 | 51 |  | 3 |  | 59 |
| 1933 | 5 | 46 |  | 3 | 1 | 55 |
| 1934 | 4 | 39 | 1 | 4 | 1 | 49 |

LOSSES BY RESIGNATION AND DEATH

|  | As | A | I | S | Resigned | Deceased |
|---|---|---|---|---|---|---|
| 1932 ......... | 1 | 18 | 1 |  | 16 | 4 |
| 1933 ......... |  | 24 | 1 | 2 | 23 | 4 |
| 1934 ......... | 1 | 18 | 1 | 3 | 19 | 4 |

| | NEW MEMBERS | | | | | SUMMARY, PAID-UP MEMBERS | | |
|---|---|---|---|---|---|---|---|---|
|  | As | A | I | S | SI | Gain | Loss | Net |
| 1932 ......... | 3 | 36 | 2 |  |  | 41 | 79 | -- 37 |
| 1933 ......... | 1 | 24 | 1 | 3 | 1 | 30 | 82 | — 52 |
| 1934 ......... | 2 | 67 | 1 | 7 |  | 77 | 72 | + 5 |
| 1935 ......... |  | 37 |  | 2 |  | 39 | 9 | .... |
| (incomplete) | | | | | | | | |

[Present membership, March 1, 1935, not including 49 members in arrears for 1934 dues, is 537.]

A. G. VESTAL, *Secretary*

The report upon motion duly made and seconded, was accepted. Dr. Alfred Emerson expressed appreciation of the efforts of the Secretary in adding to the membership of the Society.

## REPORT OF THE BUSINESS MANAGER OF ECOLOGY

The following report was presented by Dr. Gager, Business Manager of ECOLOGY, and on motion by Dr. A. H. Wright seconded by Dr. Alfred Emerson was accepted and approved.

### REPORT FOR THE FISCAL YEAR ENDING NOVEMBER 30, 1934

*Receipts*

| | | |
|---|---|---|
| Cash on hand (statement of 1933) ........................... | | $ 899.70 |
| Dr. Arthur G. Vestal, treasurer, E.S.A.: | | |
| 483 members @ $3.00 ............................ | $1,449.00 | |
| 6 institutional members @ $4.00 ................... | 24.00 | |
| 1 institutional member (½ yr.) .................. | 2.00 | 1,475.00 |
| Subscriptions, 1934 .............................. | $1,353.29 | |
| Subscriptions, 1935 .............................. | 383.50 | 1,736.79 |
| Single numbers and back volumes ....................... | | 156.70 |
| Authors' payments ................................... | | 233.18 |
| National Academy of Science—Grant ..................... | | 500.00 |
| Remittances for subscriptions to A. J. B., Genetics, and Ecological Monographs, included in checks issued to ECOLOGY .......... | | 19.65 |
| Interest on check held for collection ....................... | | .10 $5,021.12 |

*Disbursements*

Printing

     Lancaster Press, Inc. ..................................... $2,717.68

Illustrating

     Jahn & Ollier Engraving Co. ..................... $ 102.13

     Revere Photo Engraving Co. .....................     79.90     182.03

Advertising ............................................... 133.37

Office Expenses

     Clerical Assistant for 12 months @ $10.00 ......... $ 120.00

     Stationery ...................................... 32.50

     Postage Business office ......................... 77.00

     Postage Editorial office ........................ 24.50

     Wrapping paper and twine ....................... 11.73

     Express ........................................ 6.16     271.89

Miscellaneous

     Refunds on subscription and single number ......... $    5.00

     Government tax on checks .......................    .96

     Collection charges .............................    .64

     Paid to A.J.B., Genetics, and Ecological Monographs

         for subscriptions included in remittances to

         Ecology .................................. 19.65

     Registration Fee—scientific meeting .............. 1.00    27.25

       Balance November 30, 1934 ......................... $1,688.90

                                          $5,021.12

Examined and found correct, Dec. 11, 1934.

                                 H. P. SCHOENBERNER,

                                          *Auditor.*

## ASSETS AND LIABILITIES

*Assets*

Cash in Bank ...................................... $1,688.90

Bills Receivable

     Balance due on back volume ............................. $    .80

     Subscriptions, 1934 .................................... 4.14

     Subscriptions, 1935 .................................... 99.60 $ 104.54

                                          $1,793.44

*Liabilities*

Bills Payable

     Lancaster Press, Inc.

         Reprints (in part) Oct. issue ................ $   17.04

     Revere Photo Engraving Co. ..................... 48.43 $   65.47

Assets over Liabilities ......................................... 1,727.97

                                          $1,793.44

*Circulation Data as per Mailing Lists of October, 1934*

| | 1933 | 1934 |
|---|---|---|
| 1. Members | 406 | 456 |
| 2. Subscribers | 425 | 424 |
| 3. Exchanges | 97 | 93 |
| 4. Advertisers | 13 | 12 |
| 5. Editorial office | 2 | 2 |
| | 943 | 987 |
| Number of copies printed per month | 1,275 | 1,175 |

(Signed) C. STUART GAGER,

*Business Manager of Ecology*

## REPORT OF THE EDITORS OF ECOLOGY

We have been able to publish 456 pages this year as compared to 420 last year. Manuscripts accumulated as a result of the curtailments of recent years have now largely been published, and prompt publication is assured for the year 1935. We also feel that the rigid restrictions on the number of pages and illustrations adopted two years ago are no longer necessary and we suggest a much more elastic policy for the coming year. Under some circumstances, it seems feasible to accept papers of twenty printed pages. We also think that the journal may well open its pages to some authors who are not members of the society but who have interesting contributions in the field, thus returning to the pre-depression policy. We believe that there should be no lowering of standards as the result of the more satisfactory financial condition of the journal, and shall attempt to maintain the current excellence of the published contributions.

Owing to the financial condition of the journal during the depression years, the editors have made no requests for financial assistance in handling the office routine and correspondence. In conference with the Business Manager, we hope that a reasonable expenditure may be allowed us for such work.

On the whole, we feel that the journal is in a healthy state and, with the lessening financial difficulties, we definitely expect to see an improvement in service to authors within the next few years as well as an increasingly influential periodical in the field of ecology.

(Signed) ALFRED EMERSON, GEORGE D. FULLER.

On motion duly seconded the report of the Editors of ECOLOGY was approved, and their work commended.

## REPORT OF THE EDITORS OF ECOLOGICAL MONOGRAPHS

### *December 21, 1934*

On behalf of Mr. R. O. Rivera, Executive Secretary, Duke University Press, and Business Manager of ECOLOGICAL MONOGRAPHS, we present the following report for ECOLOGICAL MONOGRAPHS from December 1, 1933 to November 30, 1934:

| *Income:* | | *Expense:* | |
|---|---|---|---|
| Advertising | $ 643.83 | Advertising | $ 370.77 |
| Subscriptions | 1,301.68 | General Expense | 10.92 |
| | | Postage | 5.82 |
| | | Printing | 3,267.84 |
| | $1,945.51 | | $3,655.35 |

*Deficit* ........................... $1,709.84

The circulation of this journal is as follows:

| | |
|---|---|
| Paid subscriptions | 173 |
| Duke University Library exchange | 24 |
| Free exchange and complimentary | 17 |
| | 214 |

(Signed) A. S. PEARSE, C. F. KORSTIAN, *Editors*

Dr. Korstian added comments upon the unsatisfactory financial status of ECOLOGICAL MONOGRAPHS and recommended that efforts be made to improve this condition.

The report of the Editors of ECOLOGICAL MONOGRAPHS was approved, with expression of appreciation to them and to Duke University.

## REPORT OF THE COMMITTEE ON NOMENCLATURE

The committee has continued its work according to the policies outlined by the Society (ECOLOGY **17**: 437–438, 1931), and the principles and procedure described in previous reports (*Bull. Ecol. Soc.* **12**: 9–10, 1931; *Science* **74**: 648, 1930; ECOLOGY **13**: 205–206, 1932; and **15**: 211–212, 1934).

Preliminary List of Ecological Terms No. 1, submitted to the Society last year, has been widely distributed. The numerous suggestions received have led to further study and revision of most of the terms in the list. Many additional terms were suggested for inclusion in the next list. Two lists of definitions prepared during the year are now submitted to the Society. Revised List No. 1 is mostly made up of terms which received additional study following their presentation a year ago. Preliminary List No. 2 contains the first draft of definitions of terms most of which were suggested to the committee for inclusion in its next report. The members of the committee invite as many suggestions as possible on terms in both lists, to aid them in formulating better definitions.

Members of the Ecological Society may obtain a mimeographed copy of each list from the chairman, at the North Dakota Agricultural College, Fargo. Please enclose a 3c stamp for each list.

HERBERT C. HANSON (*Chairman*), A. S. PEARSE, C. F. KORSTIAN,
P. S. WELCH, Z. P. METCALF

The report was approved. The committee was commended for its excellent work, and was continued with the same personnel.

## REPORT OF THE COMMITTEES ON THE STUDY AND PRESERVATION OF COMMUNITIES

*1. Study of Plant and Animal Communities.*—The committee prepared a report to the Division of Biology and Agriculture of the National Research Council covering reasons for organizing the study of grassland, and a statement of opportunities for cooperation with the Federal Government, accompanied by a map. The selection of areas of submarginal land suitable for ecological study was undertaken in Illinois and in Iowa. These were presented to the Beck Committee through the hands of the state authorities to President Roosevelt's Scientific Advisory Committee, and later to the Biological Survey through the National Research Council. The Council has been repeatedly urged to find funds to stimulate legislatures to appropriate money to buy suitable lands for study in locations close to the State Universities.

*2. The Committee on the Preservation of Natural Conditions.*—During the year the Washington member (Dr. Griggs) attended two important Congressional hearings having to do with wild life restoration. The committee cooperated with the National Park Association in acting to preserve certain portions of the proposed *Everglades Park* in a natural state. The Nature Sanctuary memorandum has been sent to the Conservation Commissions of 30 states with letters urging the putting into effect of the ideas embodied in it.

*3. General Comments on the Two Committees.*—It is now five years since the Chairman of the two committees was asked to reorganize the work of the society on the preservation of natural biological condition in reservations of all kinds. The first year was devoted to extended correspondence to ascertain a method of organization. Four years have been spent in trying out this organization. It consists of a large committee, the study committee composed of men of experience well scattered through the United States and Canada representing natural districts in a general way. Various of these men are in government service. Although their opinions are especially valuable they cannot have their names used in letters to legislators, government officials, etc. The group has been used to work out general policies.

A small group representing various fields of knowledge, and including one representative in Washington has constituted the nucleus of the Com-

mittee on the Preservation of Natural Conditions. They have drafted letters and resolutions sent to government officers and attended hearings. Attached to this committee are two or more representatives in each state, province, and forest district, who may be called upon to write letters urging desired legislative or executive action. These representatives provide a list of societies interested in the Ecological Society's program. This cooperation has proved useful and effective in various cases. Once organized this group can keep alive the idea of keeping natural areas intact. To change it means a large amount of labor.

The organization has been quite successful, but the chairman asks to be relieved of any aggressive work except in connection with the grassland study project or where the advice of the study committee or some similar group is needed. The chairman will therefore continue the grassland work under the study committee, while Dr. Cahn, the secretary of the preservation committee is willing to take charge of all other work during 1935.

The chairman further requests the appointment of a committee composed of Professor Francis Ramaley (Chairman), B. C. Tharp, Albert H. Wright and Lee R. Dice, to consider whether the Society shall continue the activities represented by these committees, and if so what statement of the fact be embodied in the constitution of by-laws of the Society as a guide to future action. The committee shall be asked to recommend a plan of action for 1936 and to report to the Executive Council of the society on or before October 1, 1935.

Respectfully submitted,

V. E. SHELFORD.

The Society voted that the two committees be continued, with Dr. A. R. Cahn as Executive Secretary. It was moved and voted that the committee be appointed with Dr. Francis Ramaley as chairman, to consider future activities of the two committees, and to make recommendations to the Executive Committee of the Society.

### REPORT OF THE NOMINATING COMMITTEE

Your committee offers the following nominations:

*For President:* W. P. Taylor.
*For Vice-President:* E. Lucy Braun.
*For Secretary-Treasurer:* A. G. Vestal.
*For the Editorial Board of Ecology:* L. R. Dice, Z. P. Metcalf, L. A. Kenoyer and G. A. Pearson.
*For the Editorial Board of Ecological Monographs:* W. C. Allee and E. N. Transeau.

Your committee recommends that the present designation of "Editor and Associate Editor" of ECOLOGY be changed to "Joint Editors."

Your committee recommends the election of Alfred E. Emerson as Joint Editor of ECOLOGY.

Your committee recommends that the editors of ECOLOGICAL MONOGRAPHS be designated " Joint Editors."

Your committee recommends that W. S. Cooper be appointed to represent the Ecological Society at the Sixth International Botanical Congress, to be held at Amsterdam in September 1935, and that H. S. Conard be appointed alternate.

<div style="text-align:center">

(Signed) EDWIN B. POWERS, *Chairman,*

G. E. NICHOLS,

A. O. WEESE.

</div>

The report of the Nominating Committee was considered in detail. There being no nominations from the floor the Secretary was instructed to cast the vote of the Society for the persons designated by the Nominating Committee. The vote was cast and the officers nominated were declared elected.

By motion duly seconded and passed the recommendations of the Nominating Committee were approved and adopted.

<div style="text-align:center">

REPORT OF THE COMMITTEE ON RESOLUTIONS

</div>

Your committee offers the following resolutions:

1. The Ecological Society of America meeting with the American Association for the Advancement of Science expresses its appreciation to the local Committee for its thoughtfulness in providing all necessary arrangements for the meetings and for the annual dinner, and to the University of Pittsburgh for its provision of meeting places.

2. That we are greatly indebted to our President and Secretary for the efficient manner in which the program for the meeting has been planned and carried out.

3. That the Society thanks the chairman and members of committees which have been active during the past year, commending especially the valuable and laborious work of the Committee on Nomenclature and the Committee on Preservation of Natural Areas, and we favor their continued activity.

4. That we endorse most fully all movements for the preservation of natural areas for purposes of study, realizing that the importance of such preservation needs to be made known both to the scientific world and to the general public. Peat deposits, lake and marsh areas of all sorts are valuable in helping to maintain the water table which has been so greatly lowered in many places during the past few years. Peat land should be protected from burning and over-drainage. We urge that all government agencies cooperate in conservation of peat resources and in the preservation of marsh areas as well as extensive areas of forest and grassland.

5. That the Secretary of the Ecological Society transmit copies of these resolutions to the Secretary of Agriculture, the Secretary of the American Association for the Advancement of Science and to others having influence with governmental agencies.

Respectfully submitted,

(Signed) E. Lucy Braun, Henry J. Oosting,

Francis Ramaley *(Chairman)*.

The report of the Committee on Resolutions was unanimously approved and voted by the members present.

The business meeting of the Ecological Society adjourned at 5:50 p.m.

A. G. Vestal, *Secretary.*

# NOTES AND COMMENT

## STOMATAL FREQUENCY IN CEREALS

The purpose of this study was to find the effect of various percentages of soil moisture on the number of stomata per unit area in leaves of barley, wheat, and corn grown under greenhouse conditions. Most of the investigators of the past twenty years (see among others Maximov,[1] Bruner and Weaver,[2] and Salisbury[3]) have reported a decrease in number of stomata per unit area of leaf surface with an increase in soil moisture. Duggar[4] has reported opposite results in experiments on wheat and corn. His cultures, however, seem to have been made in sand containing 11 per cent or more of water and hence it is probable that none suffered from a deficient supply of soil moisture.

The soil used in the present experiment had a willing coefficient of 18 per cent and cultures were made with amounts of soil moisture varying from 11 to 38 per cent; therefore, some of the plants were often in a wilted condition.

Seeds of barley, wheat, and corn were placed in moist chambers and after germination were transferred to pots of soil, and the water supply was kept fairly constant and at various percentages above and below the wilting coefficient.

During the fourth week data were secured on the general appearance of the plants, on the number of suckers, on the length of leaves, and on the width of leaves. Stomatal frequency and the measurements of the stomata and typical cells were made during the fifth week. This was done by making collodion films as described by Long and Clements.[5]

The main results are as follows: too much (38 per cent) and too little (11–14 per cent) soil moisture produced inferior plants, the former probably due to poor aeration of the soil, the latter to lack of water. The intermediate percentages of soil moisture produced good plants. The best plants had the best general appearance, the longest and widest leaves, and the smallest number of stomata per unit area of leaf surface. It was also found, by measuring typical cells in the best and in the poorest plants of barley, wheat, and corn, that the average size of the cells was greater in the best plants. In general, the ratio between the length of the cells of the best and the poorest plant, was 10 to 7 for barley, 2 to 1 for wheat, 8 to 5 for corn; the width of cells, 4 to 3 for barley, 6 to 6 for wheat, and 9 to 8 for corn. The length and width of the stoma varied very little except in the case of corn where the ratio was nearly 2 to 1.

The following table gives a summary of stomatal frequency with different amounts of soil moisture, each figure representing the number of stomata per unit area being the average of at least 75 counts.

[1] **Maximov, N. A.** 1929. The plant in relation to water. English translation by Yapp. 451 pp. *The Macmillan Co. New York.*

[2] **Bruner, W. E., and J. E. Weaver.** 1923. Size and structure of leaves of cereals in relation to climate. *Univ. Studies, Univ. Nebraska* 23: 163–199.

[3] **Salisbury, E. J.** 1927. On the causes and ecological significance of stomatal frequency. *Phil. Trans. Roy. Soc. London* B 216: 1–65.

[4] **Duggar, B. M.** 1911. Plant physiology. p. 92. *The Macmillan Co. New York.*

[5] **Long, F. L., and F. E. Clements.** 1934. The method of collodion films for stomata. *Amer. Jour. Bot.* 21: 7–17.

TABLE I. *Variation in stomatal frequency in response to variations in soil moisture*

| Soil moisture percentages | Stomata per unit area of leaf surface | | |
| --- | --- | --- | --- |
| | Barley | Wheat | Corn |
| 38 | 5.12 | 6.24 | 5.22 |
| 32 | 4.80 | 5.22 | 5.10 |
| 26 | 5.03 | 4.69 | 5.67 |
| 20 | 4.96 | 5.01 | 5.05 |
| 17 | 6.24 | 6.15 | 5.20 |
| 14 | 7.25 | 6.50 | 7.46 |
| 11 | 7.55 | 7.73 | 7.78 |

In explanation of this variation of stomatal frequency it is evident that there is a low frequency under optimum conditions because the epidermal cells are larger and hence there is a greater distance between the stomata. Evidently the ratio of the number of stomata to that of epidermal cells remains about constant under all the conditions of the experiment. Hence with deficient moisture epidermal cells are smaller, more numerous per unit area, and stomatal frequency is higher than with optimum water supply. The same results seem to follow other conditions unfavorable to optimum growth.

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## MEMBERSHIP IN THE ECOLOGICAL SOCIETY OF AMERICA

The interest of the whole country is concentrated on problems of conservation and management of natural resources as never before. Almost every phase of the national conservation program involves ecological information, whether the problem be erosion control, reforestation, range rehabilitation, soil conservation or wildlife management. The important decisions are bound to be of an ecological character. There is an outstanding need, furthermore, for better correlation of activities now being conducted by a variety of agencies, private and public. The need was never more acute for competent ecologists with a point of view embracing both plants and animals as related to their environment and the ability to make economic application of their knowledge. Those responsible for the curricula of the various institutions of higher learning, especially in agriculture, conservation, range management, wildlife protection, and forestry, might well critically re-examine their courses of instruction with the object of suiting them to the needs of the hour.

The demand for a greater number of capable research workers with the ecological point of view is not limited to the field of immediate economic application. The vast majority of contributions in natural history for perhaps a couple of thousand years have been analytical in character. There is great need, however, for increased attention to synthetic phases of the various communities of plants and animals as related to their environment. Analysis is good and cannot and should not be overlooked, but synthesis is also important. William Morton Wheeler and others, in their discussions of what Wheeler calls "emergent evolution," have pointed out that a community of organisms as a whole possesses attributes of a somewhat different character than those of the organisms composing it. It is impossible to predict the characteristics of a biotic community from a study of its constituent species. It is with these whole communities of plants and animals in their environment that we largely have to deal, whether from an economic or a theoretical standpoint.

Seemingly ecology is the science which more than any of the others deals with these

important problems of the biotic community as a whole in its environment. The importance and the economic and theoretical value of work in this field cannot easily be overemphasized.

There is a most unfortunate tendency evident to carry forward far-reaching programs of management and administration of natural resources of all sorts without a proper research background. Ecologists are well aware how limited is our information, how empiric most of our applications. The need is critical for domesticating among influential people an attitude of appreciation for research, and a lively sense of the pressing need for more of it, especially, just now, along ecological lines.

Cannot the Ecological Society of America increasingly assume responsibility for encouraging the adequate training of workers with the broad ecological point of view, and for maintaining and increasing the amount of fundamental ecological research work being done? Does the Ecological Society not have also an opportunity to correlate and coordinate, in some degree, the activities of many workers so that the greatest advances can be made? If the society, through its meetings and its publications, is to perform this service in any adequate way, it must have *more members.*

The executive board would appreciate it if all members of the Ecological Society would give this matter their most earnest attention. Doubtless many of our colleagues on the faculties of the various educational institutions or in the various departments of local, state, or federal governments would be willing to affiliate with us if invited to do so. Some of the more serious-minded students, especially graduate students, are also in a position to join the society. Every technical worker who is in any way concerned with the national conservation program or with the theoretical aspects of modern scientific natural history would benefit from close contact with the members of the Ecological Society and their work. Such contact can be best assured through membership in the Ecological Society, attendance at its meetings, and reading of its publications.

WALTER P. TAYLOR

U. S. BIOLOGICAL SURVEY AND UNIVERSITY OF ARIZONA,
    TUCSON, ARIZONA
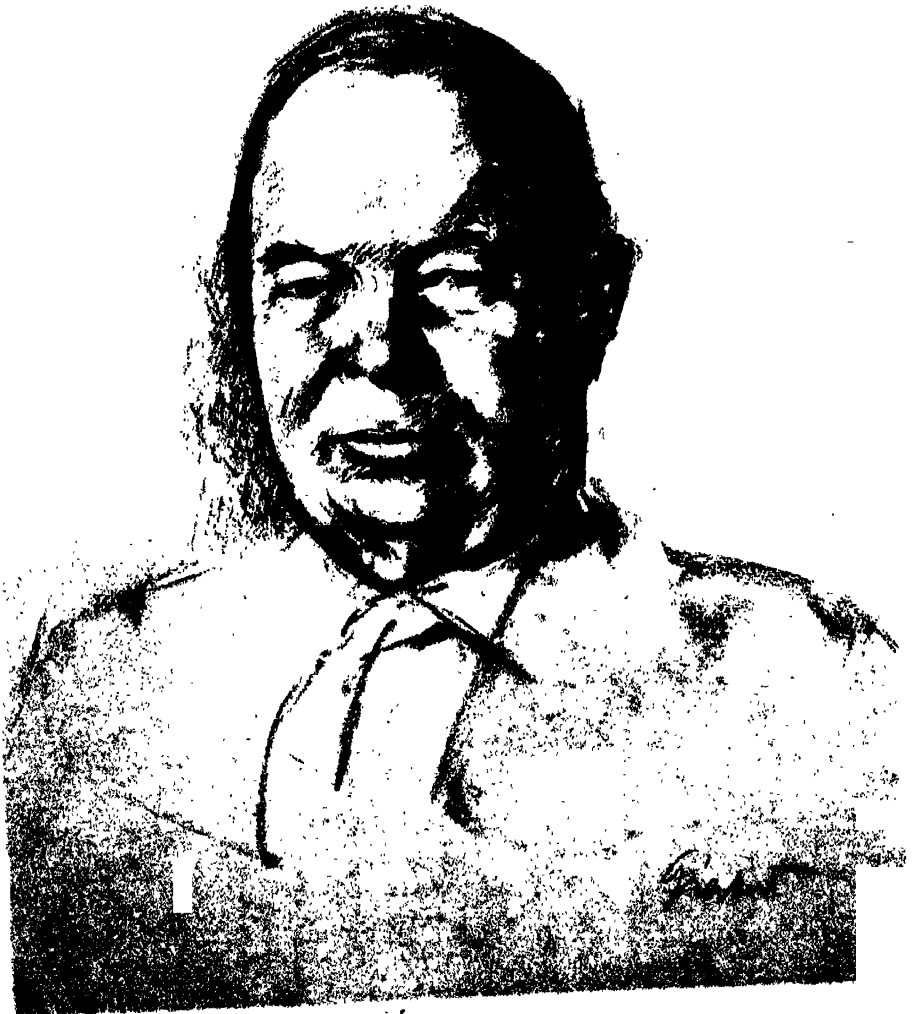
Henry C. Cowles

# ECOLOGY

## HENRY CHANDLER COWLES

Science, in its historical aspect, may be likened to a tree, constantly branching as the sum total of knowledge grows steadily greater and subdivision of the field becomes necessary. Occasionally a bud of special vigor makes its appearance and gives rise to a branch so dominating that it changes profoundly the contour of the whole organic body. In the science of vegetation, this happened when. Humboldt first stressed climate as a causative factor, and again when Grisebach formulated the concept of the plant community. Quite recently—within the memory of the older ones among us—a particularly vigorous branch has appeared—the dynamic viewpoint. For many decades the bud that produced it had lain dormant. Several times, under the ever increasing environmental influence of Darwinian thought, it tried to break through; with Warming and Schimper it almost succeeded. Finally, in the late nineties, it penetrated the overcrusting bark and shot up into a lusty limb, which today gives abundant promise that it will in time determine the whole form of the tree.

The most potent influence—enzyme, hormone, or what you will—that brought about this sudden burgeoning was the early work of Henry Chandler Cowles. He was not, however, from the beginning a botanist. His first work at the University of Chicago was in geology, in the prosecution of which he came under the potent influence of Thomas C. Chamberlin and Rollin D. Salisbury, energetic exponents of the dynamic point of view. In the Department of Botany, under John M. Coulter, he became acquainted with the pioneer plant-ecological work of Warming. From the union of botany and physiography, fertilized by the dynamic viewpoint, came a new field for scientific exploration. Ideal materials for study—the dunes of Lake Michigan—lay close at hand. In due time emerged a classic—" The Ecological Relations of the Vegetation on the Sand Dunes of Lake Michigan." This was the first comprehensive study of dune phenomena produced in America, and in it the close relations in general between physiography and vegetation were for the first time pointed out. As for its style, would that every candidate for the doctorate, before beginning to write, might be required to make a careful study of this paper!

The pioneer work on the dunes was necessarily limited in scope, and Cowles accordingly undertook a more comprehensive study, in an attempt to determine to what extent the viewpoint and method introduced in the study of the dunes were generally applicable. The resulting publication, " The Physiographic Ecology of Chicago and Vicinity," formulates a philosophy of vegetation in which the central principle is that " a classification to be true must be genetic and dynamic." In this paper the concepts of succession and climax find their first adequate expression.

The principles here enunciated, to a remarkable degree, have stood the test of time. The promulgator of new ideas is frequently tempted to go too far, to erect a " system " that is rigid and not easily modifiable when new facts appear, and which must later be partially demolished in order that a' firm foundation for future construction may be assured. This pitfall Cowles avoided. He was always cautious, never dogmatic. For example, in formulating the concept of the climax, he entertained for that state no illusion of permanency: " The condition of equilibrium is never reached, and when we say that there is an approach to the mesophytic forest, we speak only roughly and approximately. As a matter of fact we have a variable approaching a variable rather than a constant."

It is no detraction from the credit due to Cowles to recognize the fact that other men, at the same time, were thinking toward similar conclusions. The influence of Darwin's work was slowly permeating the entire body of man's thought, and its transforming effects upon the science of vegetation could not have been much longer delayed. In particular we must pay tribute to Clements, to whom had come, quite independently, the same realization of the fundamental importance of the dynamic viewpoint that had been an inspiration to Cowles.

In another and quite distant portion of the field, ecological philosophy owes much to the sane thinking of Cowles. The problem of adaptation has long been, and continues to be, one of the most difficult, and, at the same time, one of the most appealing, in all biology. During the latter half of the nineteenth century, due to the work of Kerner and others, interest in this field was widespread. The general viewpoint, however, was unfortunate. Teleology and anthropomorphism were rampant. At the turn of the century a saner attitude began to make way, but the older viewpoint was too romantically attractive to be easily displaced. As a matter of fact, it still persists in many quarters.

In 1911 appeared the " Chicago Text Book of Botany," to which Cowles contributed the second volume, dealing with ecology. Only a portion of the field was covered, namely, the branch commonly known as autecology. It was the first general treatment of this subject in America, its only predecessor in the field being the great work by Haberlandt. It differed from the latter in being fitted for the use of beginning students; at the same time it

was comprehensive in scope and contained much that was new. Most significant was the basic viewpoint, which was " that of mechanical causation rather than of teleology and adaptation "—an emphasis salutary and much needed. An attempt was made to exclude every term having in it the slightest tinge of teleology—actually an impossible task, considering the thorough way in which the language is shot through with imagery. As an endeavor toward an ideal, however, the effort was well worth while.

Fully as important as his own research has been the influence of Cowles in inspiring research by others. This became evident very early in his career, when there gathered about him a group of men scarcely younger than himself, who enthusiastically entered with him the fresh field of dynamic ecology and applied the principles he was formulating to new regions. Not all of these continued to specialize in ecology, but all gladly acknowledge the influence of his infectious enthusiasm. Since those early days many scores of graduate students have served their research apprenticeship under his direction, and have acquired from him a new ardor in creative work and a sanely progressive outlook upon the problems of science.

Even greater is the number of teachers who have learned from him how to use the out-of-doors, how to bring their pupils directly to nature, and, above all, how to unfold to them the myriad mysteries of biology without recourse to the cheap and easy fallacies of anthropomorphism.

A man may be a great scientist and a great teacher and yet inspire in his colleagues and students little affection or none at all. With Cowles it is far otherwise. Something more than mere respect for high scientific attainment is necessary to account for the fact that, when the plan for this special number of ECOLOGY was made public, more than three hundred persons responded. With almost every contribution came a letter expressing admiration for Cowles as a scientist, as a teacher, and, above all, as a man. These facts speak for themselves; formal tribute is superfluous. And yet, merely because it is a joy to do so, we make mention of a few of his many lovable traits—his unfailing good humor, his far-famed ability in the telling of a story, his readiness to give ungrudgingly of time and effort in the service of students and friends, his eagerness to discover and commend whatever is meritorious in the work of a fellow scientist or admirable in the man himself.

He may relinquish his active labors secure in the consciousness of work well done, confident of achievement beyond the ordinary lot. He has laid the foundation for a new and useful branch of science, he has constructively influenced the thought of hundreds of investigators and teachers, and in his professional and personal contacts he has made for himself a multitude of devoted friends. Fortunate and happy is the man with a record of accomplishment so thoroughly satisfying. Such good fortune and such happiness are the undoubted right and privilege of Henry Chandler Cowles.

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# THE USE AND ABUSE OF VEGETATIONAL CONCEPTS AND TERMS

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## CONTENTS

It is now generally admitted by plant ecologists, not only that vegetation is constantly undergoing various kinds of change, but that the increasing habit of concentrating attention on these changes instead of studying plant communities as if they were static entities is leading to a far deeper insight into the nature of vegetation and the parts it plays in the world. A great part of vegetational change is generally known as *succession*, which has become a recognised technical term in ecology, though there still seems to be some difference of opinion as to the proper limits of its connotation; and it is the study of succession in the widest sense which has contributed and is contributing more than any other single line of investigation to the deeper knowledge alluded to.

It is to Henry Chandler Cowles that we owe, not indeed the first recognition or even the first study of succession, but certainly the first thorough working out of a strikingly complete and beautiful successional series (1899), which together with later more comprehensive studies ('01, '11) brought before the minds of ecologists the reality and the universality of the process in so vivid a manner as to stimulate everywhere—at least in the English-speaking world—that interest and enthusiasm for the subject which has led and is leading to such great results. During the first decade of this century indeed Cowles did far more than any one else to create and to increase our knowledge of succession and to deduce its general laws. By acute and thorough observation and by lucid exposition he became the great pioneer in the subject. It is therefore natural and fitting that my contribution to a volume

intended to express the honour and affection in which Cowles is held by his fellow botanists should deal with this subject.

In 1920 and in 1926 I wrote general articles ('20, '29)[1] on this and some related topics. My return to the subject to-day is immediately stimulated by the appearance of Professor John Phillips' three articles in the *Journal of Ecology* ('34, '35) which seem to me to call rather urgently for comment and criticism. At the same time I shall take the opportunity of trying to clarify some of the logical foundations of modern vegetational theory.

If some of my comments are blunt and provocative I am sure my old friend Dr. Clements and my younger friend Professor Phillips will forgive me. Bluntness makes for conciseness and has other advantages, always provided that it is not malicious and does not overstep the line which separates it from rudeness. And at the outset let me express my conviction that Dr. Clements has given us a theory of vegetation which has formed an indispensable foundation for the most fruitful modern work. With some parts of that theory and of its expression, however, I have never agreed, and when it is pushed to its logical limit and perhaps beyond, as by Professor Phillips, the revolt becomes irrepressible. But I am sure nevertheless that Clements is by far the greatest individual creator of the modern science of vegetation and that history will say so. For Phillips' work too, and particularly for his intellectual energy and single-mindedness, I have a great admiration.

Phillips' articles remind one irresistibly of the exposition of a creed—of a closed system of religious or philosophical dogma. Clements appears as the major prophet and Phillips as the chief apostle, with the true apostolic fervour in abundant measure. Happily the *odium theologicum* is entirely absent: indeed the views of opponents are set out most fully and fairly, and the heresiarchs, and even the infidels, are treated with perfect courtesy. But while the survey is very complete and almost every conceivable shade of opinion which is or might be held is considered, there is a remarkable lack of any sustained criticism of opponents' arguments. Only here and there, as for instance in dealing with Gillman's and Michelmore's specific contentions, and in a few other places, does the author present scientific *arguments*. He is occupied for the most part in giving us the pure milk of the Clementsian word, in expounding and elaborating the organismal theory of vegetation.

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[1] The latter was not published till 1929 owing to the long delay in the appearance of the Proceedings of the International Congress of Plant Sciences at Ithaca, N. Y. It was unfortunate too that certain misprints appeared in the paper because the proof corrections were not incorporated in the published text. Since some of these misprints destroy the sense intended it may be useful to call attention to them here.

P. 677, third line from bottom: Insert "these" after "All".
P. 684, line 2: delete second comma.
P. 685, line 2: for "criticism" read "criterion".
      line 13: for "cause" read "causes".
      line 14, third word from end; for "of" read "on".

This exposition, with its very full citations and references, is a useful piece of work, but it invites attack at almost every point.

The three articles are respectively devoted to " Succession," " Development and the Climax" and " the Complex Organism." The greater part of the third article is mainly concerned with the relation of this last concept to the theory of " holism " as expounded by General Smuts and others, and is really a confession of the holistic faith. As to the repercussions of this faith on biology I shall have something to say in the sequel. But first let me deal with " Succession " and " Development and the Climax."

## SUCCESSION

My own views on succession are given fairly fully in my two papers already mentioned. In the first place I consider that the concept of succession can be given useful scientific signifiance only if we can trace in the sequences of vegetation " certain uniformities which we can make the subject of investigation, comparison, and the formulation of laws " ('29). In a paper also read at the Ithaca Congress, Cooper ('26) takes the view that since succession is the universal process of vegetational change " all vegetational changes must of necessity be successional." But I think the concept of succession involves not *merely* change, but the recognition of a *sequence of phases* (admittedly continuous from one phase to another) subject to ascertainable laws: otherwise why do we employ the term succession instead of change? And also I cannot admit that catastrophic changes due to external factors form parts of succession. Suppose an area of forest ($A$) to be suddenly invaded and devastated but not completely destroyed by a herd of elephants which then departs to other feeding grounds. Suppose that after partial regrowth ($B$) the vegetation of the same area is completely destroyed by a volcanic eruption and that on the volcanic ash which has buried $B$ a new vegetation ($C$) appears. Can $A$, $B$ and $C$ be usefully regarded as parts of *any* succession? Cooper calls the catastrophes " landmarks." I should say they were clearly *interruptions,* each initiating a new succession (sere). I think Cooper is somewhat obsessed by his image of universal vegetational change as a " braided stream," just as Clements and Phillips are obsessed by their " complex organism." A stream is continuous, *therefore* all vegetational change must also be continuous. Succession (according to my definition) *is* continuous, but it may be interrupted by catastrophes unrelated to successional processes, which last are subject to ascertainable laws. The stream analogy has its points, particularly the separation and re-uniting of currents, but it breaks down as applied to the entire history of vegetation on the earth, just because of the catastrophes; nor do I find it constructively very helpful in considering the processes of succession itself.

In 1926 (p. 680) I proposed to distinguish between *autogenic succession,* in which the successive changes are brought about by the action of the plants

themselves on the habitat, and *allogenic succession* in which the changes are brought about by external factors. " It is true of course (I wrote) and must never be forgotten, that actual successions commonly show a mixture of these two classes of factors—the external and the internal " (p. 678). I think now that I should have gone farther than this and applied my suggested new terms in the first place to the factors rather than to the successions. It is the fact; I think, that autogenic and allogenic factors are present in all successions; but there is often a clear preponderance of one or the other, and where this is so we may fairly apply the terms, with any necessary qualifications, to the successions themselves. I went on to contend, as indeed I had already done in 1920 (pp. 136–9) though without using the terms, that only to autogenic succession can we apply the concept of development of what I called a " quasi-organism " (= climax vegetation), but that this developmental (or autogenic) succession is the normal typical process in the gradual production of climax vegetation.

Phillips, following Clements, contends, on the other hand, that " succession is due to biotic reactions only, and is always progressive . . . succession being developmental in nature, the process must and can be progressive only " ('34, p. 562) ; and again, " succession is the expression of development " ('35, II, p. 214).

Now here we are concerned first of all with the use of words. If we choose to confine the use of the term succession to the series of phases of vegetation which lead up to a climatic climax, for example the various " priseres " from bare rock or water to forest, then it naturally follows that the process is " progressive only." If in addition we conceive of vegetation as an organism, of which the climax is the adult and the earlier phases of the prisere are successive larval forms, then also succession is clearly " developmental in nature," is " the expression of development." But if, on the other hand, we apply the term, as I do, and as I think most ecologists naturally do, to *any* series of vegetational phases following one another in one area, repeating themselves everywhere under similar conditions, and clearly due in each case to the same or a similar set of causes, then to say that " succession must and can be progressive only," or that it is always and everywhere developmental, is clearly contrary to the fact.

Most of the controversy about the possibility of " retrogressive succession " depends simply on this difference in the use of the word. It is true that Clements ('16, pp. 146–63) successfully showed that the phenomena represented by some of the looser uses of " retrogression " were more properly described as destruction of (for example) the climax phase, or of the dominants of the climax phase, a destruction which would normally initiate a subsere leading again to the climax if the vegetation were then let alone. But if on the other hand there is what Phillips would call a " continuative cause " at work which gradually leads to the degradation of vegetation to a

lower type it seems to me that the phenomenon is properly called retrogressive succession. Here I should include the continuous effect of grazing animals which may gradually reduce forest to grassland, the gradual leaching and concomitant raw humus formation which may ultimately reduce forest to heath, gradual increase of drainage leading to the replacement of a more luxuriant and mesophytic by a poorer and more xerophytic vegetation, or a gradual waterlogging which also leads to a change of type and usually the replacement of a " higher " by a " lower " one. All these are perfectly well-established vegetational processes. To me they are clear examples of allogenic retrogressive successions, and I cannot see how their title can be denied except by an arbitrary and unnatural limitation of the meaning of the word succession. All the processes mentioned certainly involve destruction, but they also involve the invasion, ecesis and growth of new species. " Destruction " by itself is not a criterion: does not all *progressive* succession, as Cooper ('26, p. 402) has pointed out, involve constant destruction of the plants of the earlier phases?

In the discussion referred to Clements ('16, pp. 155–9) questions the reality of the retrogressive changes posited by European ecologists in the conversion of forest into heath, in the absence of violent destruction or of change of climate. Along with his insistence on the prime importance of the water-relations in succession goes a refusal to accept the possibility of a gradual change in the soil factors as a result of progressive leaching without change of climate. We may agree with Clements that strict proof of the reality of a retrogression caused in this way must be lacking unless and until we have the results of long-continued observation and properly controlled experiment with the appropriate quantitative data; and we may also agree that " biotic factors " have not always been satisfactorily excluded from the demonstration of examples supposed to be primarily due to leaching. But we can say from numerous observations in the oceanic and sub-oceanic regions of Europe that retrogression due to leaching and concomitant soil and vegetational changes is extremely probable—at least as probable as many successions which have been inferred rather than demonstrated. And to these examples I should add the retrogression of life form involved in the gradual conversion of forest to heath or grassland and of heath to grassland due to persistent grazing.

I agree with Clements that the invasion and destruction of forest (or heath) by Sphagnum bog is not properly considered as retrogression. I should call it the conquest and suppression of a " higher " type of community by a " lower " one, owing to the peculiar nature of the latter. That the power to effect this invasion and conquest is largely due to the power of Sphagnum to hold water and to carry water with it as it invades, is certainly true, and also that Sphagnum thereby establishes a new hydrophytic habitat, which may become the starting point of a new hydrarch ." prisere." But such events cannot quite be *equated,* as Clements would equate them, with

the formation of new " bare " (water) areas.   Sphagnum is after all a plant, and the dominant of very extensive and important communities.   Under certain conditions, which are due partly to climate and partly to topography, it may retain its dominance indefinitely.   I myself should not hesitate to describe it as the primary dominant of a distinct plant formation, but then I am a heretic (or should I say a schismatic?) ('20, pp. 139–145).   The weakness of this discussion of Clements, which is both able and ingenious, seems to me to reside partly in his too exclusive insistence on the water factor (which we all admit to be of prime importance), partly on his rather undiscriminating use of " destruction," but very largely on the assumption which governs the whole argument, and, as it seems to me, is quite illegitimate, that vegetation *is* an organism and therefore *must* obey the laws of development of what we commonly know as organisms.

*Catastrophic* destruction, whether by " natural " agencies or by man, does, I think, remove the phenomena from the field of the proper connotation of succession, because catastrophes are unrelated to the causes of the vegetational changes involved in the actual process of succession.   They are only initiating causes, as Clements rightly insists: they clear the field, so to speak, for a new succession.   That is why I have insisted on gradualness as a character of succession.   Gradualness in effect is the mark of the action of " continuative " causes.

### DEVELOPMENT AND THE QUASI-ORGANISM

The word development may be used in a very wide sense: thus we speak of the development of a theme or of the development of a situation, though always, I think, with the implication of becoming more complex or more explicit.   Always, too, it is some kind of *entity* which develops, and in biology it is particularly to the growth and differentiation of that peculiarly well defined entity the individual organism that we apply the term.   Hence we can perfectly well speak in a general way of the development of any piece of vegetation that has the character of an entity, such as marsh or forest, and in common language we actually do so; but we should use the term as part of the theory of vegetation, of a body of well-established and generally acceptable concepts and laws, only if we can recognise in vegetation a number of sufficiently well-defined entities whose development we can trace, and the laws of whose development we can formulate.

In 1920 I enquired whether we could recognise such entities in vegetation, and I analysed the whole topic in considerable detail and with considerable care.   To the best of my knowledge that analysis has not been seriously criticised or impugned, and I may be permitted to think it holds the field, though various divergent opinions unsupported by arguments have since been expressed.   Briefly my conclusion was that mature well-integrated plant communities (which I identified with plant associations) had enough of the characters of organisms to be considered as *quasi-organisms,* in the same way

that human societies are habitually so considered. Though plant communities are not and cannot be so highly integrated as human societies and still less than certain animal communities such as those of termites, ants and social bees, the comparison with an organism is not merely a loose analogy but is firmly based, at least in the case of the more complex and highly integrated communities, on the close inter-relations of the parts of their structure, on their behaviour as wholes, and on a whole series of other characters which Clements ('16) was the first to point out. In 1926 (p. 679) I called attention to another important similarity which, it seems to me, greatly strengthens the comparison between plant community and organism—the remarkable correspondence between the species of a plant community and the genes of an organism, both aggregates owing their " phenotypic " expression to development in the presence of all the other members of the aggregate and within a certain range of environmental conditions.

But this position is far from satisfying Clements and Phillips. For them the plant community (or nowadays the " biotic community ") *is* an organism, and he who does not believe it departs from the true faith.

Here we are back again at the question of the meanings of words. Professor Phillips writes as if he believed words to have perfectly precise and invariable meanings, and that a given verbal proposition *must* either be true or not true, whereas in fact a proposition obviously has different meanings according to the exact connotation of the words employed. The word organism can be applied very widely indeed. Thus we have Professor Whitehead's " Philosophy of Organism " and a whole school of " organicist " philosophers: many have not hesitated to call the universe an organism. Indeed it would seem from the quotations given in the Oxford " New English Dictionary " that the application of the term primarily to individual animals and plants did not begin till less than a century ago. Professor Phillips undoubtedly has some such wide conception in the back of his mind, and indeed his confession in Part III ('35) of the holistic-faith and his citations of organicist philosophers make it certain that he has. But he should remember that he is writing primarily for ecologists, who are biologists, and that the modern biologist *means* by an organism an individual, animal or plant, and would usually refuse to apply the term to anything else. At the most we may be able to get the average biologist to admit that plant (or biotic) communities have *some* of the characters of organisms, and that it may be permissible to apply to them some such term as quasi-organism. That I think would be a useful gain because I believe (with Clements and Phillips) the idea to be of great service.

There is no need to weary the reader with a list of the points in which the biotic community does *not* resemble the single animal or plant. They are so obvious and so numerous that the dissent expressed and even the ridicule poured on the proposition that vegetation *is* an organism are easily understood. Of course Clements and Phillips reply that no one asserts that the

plant community is an *individual* organism. In the more recent phrase it is a " complex organism "—a thoroughly bad term, as it seems to me, for it is firmly associated in the minds of biologists with the " higher " animals and plants—the mammals and spermaphytes. In any case it is, in my judgment, impossible to· get the proposition generally accepted. Whether it is true or untrue depends entirely on the connotation of " organism," and as to that the present generation of biologists have a firmly established use from which they will not depart—and I think they are right. We need a word for the peculiarly definite, sharply limited and unique type of organisation embodied in the individual animal or plant, and " organism " is the accepted term.

It may be said, as I imagine Cooper would say, that even such a term as " quasi-organism " is quite unnecessary if we keep the concept of " climax," which is very widely accepted. I do not agree, because climax does not suggest *organisation,* and the organisation of a mature complex plant association is a very real thing. The relatively stable climax community is a complex whole with more or less definite structure, *i.e.,* inter-relation of parts adjusted to exist in the given habitat and to co-exist with one another. It has come into being through a series of stages which have approximated more and more to dynamic equilibrium in these relations. This surely *is* " organisation," and organisation of the same type as, though by no means identical with, that of the single animal or plant. The organising factors are on the one hand the total net action of the effective environmental factors, on the other the combined actions of the individual organisms themselves. Phillips aptly quotes Karzinkin (1927) working on the " biocenoses " of animals living on water plants. Karzinkin found that changes in the external biota or in the constituents of the biocenosis disturb its equilibrium; but while the disturbance may be long-continued and complicated, equilibrium is ultimately again attained. It is possible therefore to speak of a " biocenosis " only when it reacts as a whole on the changes of the external and also of the internal factors. Cooper, who says ('26, p. 402) that progress· in vegetational change is developmental " not because the vegetation unit is an organism but because it is made up of organisms undergoing development," adds that the progress of the whole is " subject to modifications due to mass action." It is precisely this " mass action," together with the actions due to the close and often delicate interlocking of the functions of the constituent organisms, which gives coherence to the aggregation, forces us to call it a " unit," justifies us in considering it as an organic entity, and makes it reasonable to speak of the development *of* that entity.

That this " development " is something very different from the ontogeny of a plant or animal (though even here there are also striking similarities) goes without saying. The adult quasi-organism can develop from beginnings which are totally opposed—a phenomenon completely alien from the ontogeny of a plant or animal—it can be hydrarch or xerarch; and the constituents of the " developmental stages " are quite different from the constituents of the

" adult." Starting from the type of the individual organism we have here something so different that it is no wonder there is refusal to call it by the same name, but at the same time something like enough to justify a related name.

I can only conclude that the term " quasi-organism " is justified in its application to vegetation, but that the terms " organism " or " complex organism " are not.

## CLIMAXES

Professor Phillips' treatment of the concept of climax is open to nearly the same criticism as his treatment of succession. Just as he will only have one kind of succession, which is always progressive, and entirely caused by the " biotic reactions " of the community, so he will have only one kind of climax, the climatic climax, of which there is only one in each climatic region. He rather ingenuously suggests that the adjective " climatic " had better be dropped: it is misleading to the uninitiated. Since there is only one kind of climax why qualify the word? The suggestion would be unanswerable if we all agreed with him!

First there are some ecologists who believe there may be more than one climax in a climatic region, each with distinct dominants. This is the so-called " polyclimax theory," opposed to the " monoclimax " doctrine of Clements and Phillips, which supposes that there is only one " true " climax in each " climatic region," and that this should therefore be called *the* climax.

Now the so-called " polyclimax theory " takes what appear to be permanent types of vegetation under given conditions and calls them climaxes, because they are culminations of successions. The usual view is that under the " typical " climatic conditions of the region and on the most favourable soils the climatic climax is reached by the succession; but that on less favourable soils of special character different kinds of stable vegetation are developed and remain in possession of the ground, to all appearance as permanently as the climatic climax. These are called *edaphic climaxes,* because the differentiating factor is a special soil type. Similarly special local climates determined by topography (*i.e.,* land relief) determine *physiographic climaxes.* But we may go farther than this and say that the incidence and maintenance of a decisive " biotic factor " such as the continuous grazing of animals may determine a *biotic climax.* And again we may speak of a *fire climax* when a region swept by constantly recurrent fires shows a vegetation consisting only of species able to survive under these trying conditions of life; or of a *mowing climax* established as a result of the regular periodic cutting of grasses or sedges. In each case the vegetation appears to be in equilibrium with *all* the effective factors present, including of course the climatic factors, and the climax is named from the special factor differentiating the vegetation from the climatic climax. The edaphic climaxes correspond in general with Schimper's edaphic formations.

I should not myself call the usage embodied in this terminology a " theory " of any kind. It is simply an empirical terminology applied to what seem rather obvious facts of vegetational distribution. The word climax is used in its simple and natural signification of a culmination of development—a permanent or apparently permanent condition reached when the vegetation is in equilibrium with all the incident factors.

Clements realised from the first ('16) that vegetation existed which was neither climatic climax nor part of a sere actually moving towards it, but might be in a permanent or quasi-permanent condition in some sense " short of " the climax, and all such vegetation he called *sub-climax*. He used this term in two senses, for an actual seral stage which would normally lead to the climatic climax, and for a type of climax " subordinate to " the climatic climax. It was pointed out that this double use was undesirable, and that if we confined the term subclimax to the former case, terms were wanted for permanent or quasi-permanent vegetation which did not closely represent a particular phase of a sere leading to the climatic climax, but were dominated by species that did not enter into any of the " normal " seres. For such climaxes Clements has now · ('34, p. 45) proposed the word *proclimax, i.e.,* vegetation which appears *instead of* the climatic climax, or as he would say, instead of *the* climax. This I think is an unobjectionable term, but it does not specify the factors which have differentiated the different types of this sort of climax.

Godwin ('29) has insisted that the factors which prevent a sere from reaching the climatic climax not only *arrest* the sere, but also *deflect* it from its normal course, which may be re-entered when these factors are removed. He is sceptical of the existence of subclimaxes in the strict sense, and prefers to speak of " deflected succession." We might call such successions, which undoubtedly exist, *plagioseres, i.e.,* " bent " or " twisted " seres, and if the vegetation really does come into equilibrium with the deflecting factor, of a *plagioclimax,* if such terms are considered useful.

As expounded by Phillips the " monoclimax theory " explains away the existence of what some of us are accustomed to call edaphic and physiographic climaxes within a climatic region in two ways. Either these supposed climaxes are not climaxes at all but stages in a sere leading to *the* climax, whose movement has been *retarded,* perhaps for a long time, by the edaphic or physiographic factors, or they are mere variations of " the formation " (the climatic climax). It is not to be supposed and is not in fact the case, it is argued, that either climate or soil will be absolutely uniform within a great climatic region, which often extends for many hundreds of miles. The climatic formation (*the* formation according to the " monoclimax theory ") is often " a veritable mosaic " of vegetation (Clements). This of course is quite true: the only question is, *how great differences* are we to admit as mere variations within the formation? The difficulty disappears of course if we *define* a formation—a climatic climax—as *all* permanent vegetation within the climatic

region and are therefore willing to swallow such differences, however great. But is this sound empirical method? It is not rather a case of making the facts fit the theory? Is it not sounder scientific method *first* to recognise, describe and study all the relationships of actually existing vegetation, and *then* to see how far they fit or do not fit any general hypothesis we may have provisionally adopted?

Most of the kinds of vegetation which some of Phillips' colleagues in Africa consider as separate formations Phillips declares to be seral stages—examples of retarded succession, and if they are not that then they are variations of the climax. It is impossible for one who has not studied this vegetation at first hand to decide which is right—Phillips or his critics. My general impression after reading the discussion, so far as it has gone, is that not enough is known of the behaviour of the vegetation in question to enable one to be at all sure which view interprets the facts more naturally. It is possible that Phillips is right in his particular interpretations, for some of which he seems to make a good case. His general view seems to be that the so-called "edaphic climaxes" or "edaphic formations" are *never* permanent, but *always* seral stages, in which the succession may be delayed for a longer or shorter time, but which will always ultimately progress to the climatic climax. If this were true they would be excluded from Clements' category of "proclimaxes," which is intended to be applied ('34, p. 45) to climaxes produced by such allogenic factors as fire or grazing. If on the other hand edaphic factors are really capable of holding vegetation in a permanent or quasi-permanent equilibrium—and I am far from being convinced that they are not—then, as it seems to me, such vegetation is quite reasonably included in the general concept of the "proclimax," though it is clear that specific edaphic factors stand in a relationship to vegetation different from that of fire or grazing, both because they form part of the "original" environment and because they themselves usually undergo continuous change.

Here we encounter a complication which has not hitherto, so far as I know, received any adequate consideration in the literature—I mean the influence of the modern theory of soil development on the theory and classification of vegetation. It is a simple and attractive idea that development of the soil profile runs *pari passu* with development of the vegetation it bears, and that consequently the mature climatic soil type corresponds and co-exists with the climatic climax community. It is however quite premature and probably untrue to make any such general assertion. It may very well be that in particular cases such a correspondence actually exists. But on the other hand, even when profile development under the influence of climate is perfectly normal and regular, the climatic climax community may establish itself long before the soil is mature, and may not be substantially altered by the later stages of profile maturation. Again a climatic climax may establish itself on a soil which is *kept immature* by geological and physiographic causes, as on a steep slope. And finally it is now generally agreed by pedologists

that some rocks, owing to the simplicity of their composition, produce soils which can *never* form the normal climatic mature profile, and these may or may not bear the typical climatic climax vegetation. Whether any deviating communities which they may bear should be included as *parts* of the climatic climax should depend, as it seems to me, on the *extent* of that deviation. If it is wide, involving for example the dominance of different life forms, to assert that such vegetation *must* be part of the climatic climax *because* it appears in the same climatic region is surely to force the 'facts into a bed of Procrustes, to classify vegetation arbitrarily and unnaturally in the interests of a pre-conceived theory. Exactly the same is true of vegetation determined by any other edaphic factor, *e.g.,* permanent waterlogging for part at least of the year, or high soil acidity due to the poverty of the subsoil in basic ions or to the high rate of leaching in a highly permeable soil—which checks the maturation of the soil or diverts its course and thus prevents the appearance of climatic climax communities. There is no evidence that such kinds of vegetation represent stages of seres which will lead to climatic climax, nor can they be naturally regarded as parts of that climax.

On the other hand Bourne ('34) would have us regard every distinct variation of the climatic formation as a separate climax, *e.g.,* the spruce forests of the Vosges and of the Jura. No doubt they differ, as he says, quite markedly in certain. respects which may be very important to a forester and for detailed ecological studies; and they may perhaps be suitably distinguished as separate *climax sociations.* But his general view reminds one of the taxonomists who will attend to nothing but " microspecies," losing sight of the higher grades of the taxonomic hierarchy.

I have even heard the argument that immature topography, for example, the slope of a hill, bears immature vegetation, and that since the slope will eventually disappear because it will ultimately be worn down to the base level of erosion, its vegetation must be regarded as seral. But this is surely to assert that tectonic and vegetational development must always run *pari passu,* whereas their time factors are usually widely different. They are very far from always keeping step, and immature topography is actually often clothed with climax vegetation, though Cowles ('01) has cited some striking cases of correlated development between physiography and vegetation.

I plead for empirical method and terminology in all work on vegetation, and avoidance of generalised interpretation based on a theory of what *must* happen because " vegetation is an organism."

## " THE COMPLEX ORGANISM "

Professor Phillips' third article ('35, III) is devoted to a discussion of the " complex organism," otherwise known as " the biotic community " (or " biome " of Clements) in the light of the doctrines of emergent evolution and of holism. On the biotic community he had already written ('31) and so also have Shelford ('31) and others.

I have already expressed a certain amount of scepticism of the soundness of the conception of the biotic community ('29, p. 680), without giving my reasons at all fully.   It seems necessary now to state the grounds of my scepticism, and at the same time to make clear that I am not by any means wholly opposed to the ideas involved, though I think that these are more naturally expressed in another way.

On linguistic grounds I dislike the term biotic *community.*   A "community," I think it will be generally agreed, implies *members,* and it seems to me that to lump animals and plants together as *members* of a community is to put on an equal footing things which in their whole nature and behaviour are too different.   Animals and plants are not common members of anything except the organic world (in the biological, not the "organicist" sense).   One would not speak of the potato plants and ornamental trees and flowers in the gardens of a human community as *members* of that community, although they certainly enter into its constitution—it would be different without them.   There must be some sort of *similarity,* though not of course *identity,* of nature and status between the members of a community if the term is not to be divorced too completely from its common meaning. It may of course be argued by advocates of the term that the disparity of nature and behaviour between autotrophic plants and parasites—fungal or phanerogamic—is nearly as great as between animals and plants.   But it may be rejoined that " human parasites " are well known in the societies of men, and that though it may well be held that a human society would get on better without them, yet they are in some sense members of the community. Though fungi are so different from autotrophic plants that they have even been regarded as forming a third " kingdom," distinct from both animals and plants, they are at least a good deal closer to green plants than they are to animals; and parasitic phanerogams undoubtedly form a link in nature and behaviour between parasitic fungi and autophytes, while saprophytic fungi are brought within the conceptual framework as " members " of a complex community such as a forest without any violence at all.   Between all these organisms and the members of the animal kingdom there is however a very big gap in every respect.

Animal ecologists in their field work constantly find it necessary to speak of *different* animal communities living in or on a given plant community, and this is a much more natural conception, formed in the proper empirical manner as a direct description of experience, than the " biotic community."   Some of the animals belonging to these various animal communities have very restricted habitats, others much wider ones, while others again such as the larger and more active predaceous birds and mammals range freely not only through an entire plant community but far outside its limits.   For these reasons also, the practical necessity in field work of separating and independently studying the animals communities of a " biome," and for some

purposes the necessity of regarding them as external factors acting on the plant community—I cannot accept the concept of the *biotic* community.

This refusal is however far from meaning that I do not realise that various " biomes," the whole webs of life adjusted to particular complexes of environmental factors, are real " wholes," often highly integrated wholes, which are the living nuclei of *systems* in the sense of the physicist. Only I do not think they are properly described as " organisms " (except in the " organicist " sense). I prefer to regard them, together with the whole of the effective physical factors involved, simply as " *systems.*"

I have already criticised the term " organism " as applied to communities of plants or animals, or to " communities " of plants *and* animals, on the ground that while these aggregations have *some* of the qualities of organisms (in the biological sense) they are too different from these to receive the same unqualified appellation. And I have criticised the term " complex organism " on the ground that it is already commonly applied to the species or individuals of the higher animals and plants. Professor Phillips' third article ('35, III) is largely devoted to an exposition and defence of the concept of " the complex organism." According to the organicist philosophy, which he seems to espouse, though he does not specifically say so, he is perfectly justified in calling the whole formed by an integrated aggregate of animals and plants (the " biocenosis," to use the continental term) an " organism," provided that he includes the physical factors of the habitat in his conception. But then he must also call the universe an organism, and the solar system, and the sugar molecule and the ion or free atom. They are all organised " wholes." The nature of what biologists call living organisms is wholly irrelevant to this concept. They are merely a special kind of " organism."

With the philosophical aspects of Phillips' discussion I cannot possibly deal adequately here. They involve, as indeed he recognises, some of the most difficult and elusive problems of philosophy. The doctrine of " emergent evolution," stated in a particular way, I hold to be perfectly sound, and some, though not all, of the ideas contained in Smuts' holism I think are acceptable and useful. But on the scientific, as distinct from the philosophical plane, I do think a good deal of fuss is being made about very little. For example—" newness springing from the interaction, interrelation, integration and organisation of qualities . . . could not be predicted from the sum of the particular qualities or kinds of qualities concerned : integration of the qualities thus results in the development of a whole different from, unpredictable from, their mere summation." Can one in fact form any clear conception of what " mere summation " can mean, as contrasted with the actual relations and interactions observed between the components of an integrated system? Has " mere summation " any meaning at all in this connexion? What we *observe* is juxtaposition and interaction, with the resulting emergence of what we call (and I agree *must* call) a " new " entity. And who will be so bold as to say that this new entity, for example the molecule of

water and its qualities, would be unpredictable, if we really understood *all* the properties of hydrogen and oxygen atoms and the forces brought into play by their union? Unpredictable by us with our present knowledge, yes; but *theoretically* unpredictable, surely not. When an inventor makes a new machine, he is just as certainly making a new entity, but he can predict with accuracy what it will be and what it will do, because within the limits of his purpose he *does* understand the whole of the relevant properties of his materials and knows what their interactions will be, given a particular set of spatial relations which he arranges.

In discussing General Smuts' doctrine of "holism" Phillips lays stress on the whole as a *cause*, "holism" is called the fundamental factor operative towards the creation of wholes in the universe." It is an "operative cause" and an "inherent, dynamic characteristic" in communities. All but those who take "a static view of the structure, composition and life of communities—cannot fail to be impressed with the fundamental nature of the *factor of holism* innate in the very being of community, a factor of *cause*" (italics in the original).

How is this view justified? "At different levels the whole reacts upon habitat, changing (ameliorating) this for higher level wholes: the reaction of a whole, taken into account with its particular habitat and with the interrelations existing among its constituent organisms, shows as emergent changes in the habitat that are different from the sum of the changes that the constituent organisms would undergo were these not in communal association" [2] ('35, III, p. 498).

In this statement, we may note, it is not the mysterious "factor" called "holism" but the *particular* "whole" which is supposed to act as cause. Perhaps the "factor of holism" is intended as an abstraction from the effects of all the particular observed wholes. There is here again the artificial antithesis of an abstraction, "the sum of the changes that the constituent organisms would undergo" if they were not "in communal association," with what actually takes place in the community. Such a "sum" is quite unreal, there can be no meaning in considering the total activities *under unspecified conditions* of a particular lot of organisms taken together unless they *are* "in communal association." And if they are, they act upon one another, modify one another's actions, and produce new actions which are jointly dependent on two or more components. And it is precisely the sum of these modified and new actions which constitutes what we call, and rightly call, the activity of the community as a whole, because they depend upon the existence of that particular association of organisms with that particular habitat.

Is the community then the "cause" of its own activities? Here we touch

[2] Phillips however seems to think his statement is open to logical objection, but adds that "the accumulation of ecological evidence is becoming so impressive that I am not seriously perturbed by the strictures of pure logic." Surely it is his business either to show that the logic referred to is bad logic, or else to *be* "seriously perturbed" by it.

the very difficult philosophical question of the meaning of causation, which I cannot possibly attempt to discuss here. In a certain sense however, the community as a whole may be said to be the " cause " of its own activities, because it represents the aggregation of components the sum (or more properly the synthesis) of whose actions we call the activities of the community—actions which would not be what they are unless the components were associated in the way in which they are associated. So far we may concede Phillips' contention. But it is important to remember that these activities of the community are *in analysis* nothing but the synthesised actions of the components in association. We have simply shifted our point of view and are contemplating a new entity, so that we now, quite properly, regard the totality of actions as the activity of a higher unit.[8]

It is difficult to resist the impression that Professor Phillips' enthusiastic advocacy of holism is not wholly derived from an objective contemplation of the facts of nature, but is at least partly motived by an imagined future " whole " to be realised in an ideal human society whose reflected glamour falls on less exalted wholes, illuminating with a false light the image of the " complex organism."

## THE ECOSYSTEM

I have already given my reasons for rejecting the terms " complex organism " and " biotic community." Clements' earlier term " biome " for the whole complex of organisms inhabiting a given region is unobjectionable, and for some purposes convenient. But the more fundamental conception is, as it seems to me, the whole *system* (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome—the habitat factors in the widest sense. Though the organisms may claim our primary interest, when we are trying to think fundamentally we cannot separate them from their special environment, with which they form one physical system.

It is the systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. Our natural human prejudices force us to consider the organisms (in the sense of the biologist) as the most important parts of these systems, but certainly the inorganic " factors " are also parts—there could be no systems without them, and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and the inorganic. These *ecosystems*, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom. The whole method of science, as H. Levy ('32) has most convincingly pointed

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[8] If this statement is applied to the individual organism, it of course involves the repudiation of belief in any form of vitalism. But I do not understand Professor Phillips to endow the " complex organism " with a " vital principle."

out, is to isolate systems mentally for the purposes of study, so that the series of *isolates* we make become the actual objects of our study, whether the isolate be a solar system, a planet, a climatic region, a plant or animal community, an individual organism, an organic molecule or an atom. Actually the systems we isolate mentally are not only included as parts of larger ones, but they also overlap, interlock and interact with one another. The isolation is partly artificial, but is the only possible way in which we can proceed.[4]

Some of the systems are more isolated in nature, more autonomous, than others. They all show organisation, which is the inevitable result of the interactions and consequent mutual adjustment of their components. If organisation of the possible elements of a system does not result, no system forms or an incipient system breaks up. There is in fact a kind of natural selection of incipient systems, and those which can attain the most stable equilibrium survive the longest. It is in this way that the dynamic equilibrium, of which Professor Phillips writes, is attained. The universal tendency to the evolution of dynamic equilibria has long been recognised. A corresponding idea was fully worked out by Hume and even stated by Lucretius. The more relatively separate and autonomous the system, the more highly integrated it is, and the greater the stability of its dynamic equilibrium.

Some systems develop gradually, steadily becoming more highly integrated and more delicately adjusted in equilibrium. The ecosystems are of this kind, and the normal autogenic succession is a progress towards greater integration and stability. The " climax " represents the highest stage of integration and the nearest approach to perfect dynamic equilibrium that can be attained in a system developed under the given conditions and with the available components.

The great regional climatic complexes of the world are important determinants of the primary terrestrial ecosystems, and they contribute *parts* (components) to the systems, just as do the soils and the organisms. In any fundamental consideration of the ecosystem it is arbitrary and misleading to abstract the climatic factors, though for purposes of separation and classification of systems it is a legitimate procedure. In fact the climatic complex has more effect on the organisms and on the soil of an ecosystem than these have on the climatic complex, but the reciprocal action is not wholly absent. Climate acts on the ecosystem rather like an acid or an alkaline " buffer " on a chemical soil complex.

Next comes the soil complex which is created and developed partly by the subjacent rock, partly by climate, and partly by the biome. Relative maturity of the soil complex, conditioned alike by climate, by subsoil, by physiography and by the vegetation, may be reached at a different time from that at which the vegetation attains its climax. Owing to the much greater local variation of subsoil and physiography than of climate, and to the fact that some of the

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[4] The mental isolates we make are by no means all coincident with physical systems, though many of them are, and the ecosystems among them.

existing variants prevent the climatic factors from playing the full part of which they are capable, the developing soil complex, jointly with climate, may determine variants of the biome. Phillips' contention that soil never does this is too flatly contrary to the experience of too many ecologists to be admitted. Hence we must recognise ecosystems differentiated by soil complexes, subordinate to those primarily determined by climate, but none the less real.

Finally comes the organism-complex or biome, in which the vegetation is of primary importance, except in certain cases, for example many marine ecosystems. The primary importance of vegetation is what we should expect when we consider the complete dependence, direct or indirect, of animals upon plants. This fact cannot be altered or gainsaid, however loud the trumpets of the " biotic community " are blown. This is not to say that animals may not have important effects on the vegetation and thus on the whole organism-complex. They may even alter the primary structure of the climax vegetation, but usually they certainly do not. By all means let animal and plant ecologists study the composition, structure, and behaviour of the biome together. Until they have done so we shall not be in possession of the facts which alone will enable us to get a true and complete picture of the life of the biome, for both animals and plants are components. But is it really necessary to formulate the unnatural conception of biotic *community* to get such co-operative work carried out? I think not. What we have to deal with is a *system,* of which plants and animals are components, though not the only components. The biome is determined by climate and soil and in its turn reacts, sometimes and to some extent on climate, always on soil.

Clements' " prisere " ('16) is the gradual development of an ecosystem as we may see it taking place before us to-day. The gradual attainment of more complete dynamic equilibrium (which Phillips quite rightly stresses) is the fundamental characteristic of this development. It is a particular case of the universal process of the evolution of systems in dynamic equilibrium. The equilibrium attained is however never quite perfect: its degree of perfection is measured by its stability. The atoms of the chemical elements of low atomic number are examples of exceptionally stable systems—they have existed for many millions of millennia: those of the radio-active elements are decidedly less stable. But the order of stability of all the chemical elements is of course immensely higher than that of an ecosystem, which consists of components that are themselves more or less unstable—climate, soil and organisms. Relatively to the more stable systems the ecosystems are extremely vulnerable, both on account of their own unstable components and because they are very liable to invasion by the components of other systems. Nevertheless some of the fully developed systems—the " climaxes "—have actually maintained themselves for thousands of years. In others there are elements whose slow change will ultimately bring about the disintegration of the system.

This relative instability of the ecosystem, due to the imperfections of its equilibrium, is of all degrees of magnitude, and our means of appreciating and measuring it are still very rudimentary. Many systems (represented by vegetation climaxes) which appear to be stable during the period for which they have been under accurate observation may in reality have been slowly changing all the time, because the changes effected have been too slight to be noted by observers. Many ecologists hold that *all* vegetation is *always* changing. It may be so: we do not know enough either to affirm or to deny so sweeping a statement. But there may clearly be minor changes within a system which do not bring about the destruction of the system as such.

Owing to the position of the climate-complexes as primary determinants of the major ecosystems, a marked change of climate must bring about destruction of the ecosystem of any given geographical region, and its replacement by another. This is the *clisere* of Clements ('16). If a continental ice-sheet slowly and continuously advances or recedes over a considerable period of time all the zoned climaxes which are subjected to the decreasing or increasing temperature will, according to Clements' conception, move across the continent " as if they were strung on a string," much as the plant communities zoned round a lake will move towards its centre as the lake fills up. If on the other hand a whole continent desiccates or freezes many of the ecosystems which formerly occupied it will be destroyed altogether. Thus whereas the prisere is the development of a single ecosystem *in situ,* the clisere involves their destruction or bodily shifting.

When we consider long periods of geological time we must naturally also take into account the progressive evolution and rise to dominance of new types of organism and the decline and disappearance of older types. From the earlier Palaeozoic, where we get the first glimpses of the constitution of the organic world, through the later Palaeozoic where we can form some fairly comprehensive picture of what it was like, through the Mesozoic where we witness the decline and dying out of the dominant Palaeozoic groups and the rise to prominence of others, the Tertiary with its overwhelming dominance of Angiosperms, and finally the Pleistocene ice-age with its disastrous results for much of the life of the northern hemisphere, the shifting panorama of the organic world presents us with an infinitely complex history of the formation and destruction of ecosystems, conditioned not only by radical changes of land surface and climate but by the supply of constantly fresh organic components. We can never hope to achieve more than a fragmentary view of this history, though doubtless our knowledge will be very greatly extended in the future, as it has been already notably extended during the last 30 years. In detail the initiation and development of the ecosystems in past times must have been governed by the same principles that we can recognise to-day. But we gain nothing by trying to envisage in the same concepts such very different processes as are involved in the shifting or destruction of ecosystems on the one hand and the development of individual systems on the

other.   It is true, as Cooper insists ('26), that the changes of vegetation on
the earth's surface form a continuous story: they form in fact only a part of
the story of the changes of the surface of this planet.   But to analyse them
effectively we must split up the story and try to focus its phases according to
the various kinds of process involved.

## BIOTIC FACTORS

Professor Phillips makes a point of separating the effect of grazing herbiv-
orous animals *naturally* belonging to the " biotic community," e.g., the bison
of the North American prairie or the antelopes, etc., of the South African
veld, from the effect of grazing animals introduced by man.   The former
are said to have co-operated in the production of the short grass vegetation
of the Great Plains, which has even been called the *Bison-Bouteloa* climax,
and to have kept back the forest from invading the edges of the grassland
formation.   The latter are supposed to be merely destructive in their effects,
and to play no part in any successional or developmental process.   This is
perhaps legitimate as a description of the ecosystems of the world before the
advent of man, or rather with the activities of man deliberately ignored.   It
is obvious that modern civilised man upsets the " natural " ecosystems or
" biotic communities " on a very large scale.   But it would be difficult, not to
say impossible, to draw a natural line between the activities of the human
tribes which presumably fitted into and formed parts of " biotic communities "
and the destructive human activities of the modern world.   Is man part of
" nature " or not?   Can his existence be harmonised with the conception of
the " complex organism "?   Regarded as an exceptionally powerful biotic
factor which increasingly upsets the equilibrium of preexisting ecosystems
and eventually destroys them, at the same time forming new ones of very
different nature, human activity finds its proper place in ecology.

As an ecological factor acting on vegetation the effect of grazing heavy
enough to prevent the development of woody plants is essentially the same
effect wherever it occurs.   If such grazing exists the grazing animals are
an important factor in the biome actually present whether they came by them-
selves or were introduced by man.   The dynamic equilibrium maintained is
primarily an equilibrium between the grazing animals and the grasses and
other hemicryptophytes which can exist and flourish although they are con-
tinually eaten back.

Forest may be converted into grassland by grazing animals.   The substitu-
tion of the one type of vegetation for the other involves destruction of course,
but not merely destruction: it also involves the appearance and gradual estab-
lishment of new vegetation.   It is a successional process culminating in a
climax under the influence of the actual combination of factors present and
since this climax is a well-defined entity it is also the development of that
entity.   It is true of course that when man introduces sheep and cattle he

protects them by destroying carnivores and thus artificially maintains the ecosystem whose essential feature is the equilibrium between the grassland and the grazing animals. He may also alter the position of equilibrium by feeding his animals not only on the pasture but also partly away from it, so that their dung represents food for the grassland brought from outside, and the floristic composition of the grassland is thereby altered. In such ways *anthropogenic ecosystems* differ from those developed independently of man. But the essential formative processes of the vegetation are the same, however the factors initiating them are directed.

We must have a system of ecological concepts which will allow of the inclusion of *all* forms of vegetational expression and activity. We cannot confine ourselves to the so-called " natural " entities and ignore the processes and expressions of vegetation now so abundantly provided us by the activities of man. Such a course is not scientifically sound, because scientific analysis must penetrate beneath the forms of the " natural " entities, and it is not practically useful because ecology must be applied to conditions brought about by human activity. The " natural " entities and the anthropogenic derivates alike must be analysed in terms of the most appropriate concepts we can find. Plant community, succession, development, climax, used in their wider and not in specialised senses, represent such concepts. They certainly involve an abstraction of the vegetation as such from the whole complex of components of the ecosystem, the remaining components being regarded as factors. This abstraction is a convenient isolate which has served and is continuing to serve us well. It has in fact many, though by no means all, of the qualities of an organism. The biome is a less convenient isolate for most purposes, though it has some uses, and it is not in the least improved by being called a " biotic community " or a " complex organism," terms which are illegitimately derived and which introduce misleading implications.

METHODOLOGICAL VALUE OF THE CONCEPTS RELATING TO SUCCESSIONAL
CHANGE

There can be no doubt that the firm establishment of the concept of succession has led directly to the creation of what is now often called dynamic ecology and that this in its turn has greatly increased our insight into the nature and behaviour of vegetation. The simplest possible scheme involves a succession of vegetational stages (the prisere of Clements) on an initially " bare " area, culminating in a stage (the climax) beyond which no further advance is possible under the given conditions of habitat (in the widest sense) and in the presence of the available colonising species. If we recognise that the climax with its whole environment represents a system in relatively stable dynamic equilibrium while the preceding stages are not, we have already the *essential framework* into which we can fit our detailed investigations of particular successions. Unless we use this framework, unless we recognise the

universal tendency of the system in which vegetation is the most conspicuous component to attain dynamic equilibrium by the most complete adjustment possible of all the complexes involved we have no key to correct interpretation of the observed phenomena, which are open to every kind of misinterpretation. From the results of detailed investigations of successions, which incidentally throw a great deal of new light on existing vegetation whose nature and status were previously obscure, we may deduce certain general laws and formulate a number of useful subsidiary concepts. So far the concept of succession has proved itself of prime methodological value.

The same can scarcely be said of the concept of the climax as an organism and all that flows from its strict interpretation. On the contrary this leads to the dogmatic theses that development of the " complex organism " can *never* be retrogressive, because retrogression in development is supposed to be contrary to the nature of an organism, and that edaphic or biotic factors can *never* determine a climax, because this would cut across the conception of the climatic climax as *the* " complex organism."

Phillips says ('35, II, p. 242) that " the utility of the climax in Clements' sense would be greatly impaired were we to attempt to isolate from it the concept of the community as a complex organism. Its natural dynamic utility for orientation of research in succession, development and classification would be distinctly diminished." And again ('35, III, p. 503), " The biotic community is an organism, a highly complex one: this concept is fundamental to a natural setting and classification of the profoundly important processes of succession, development and attaining of dynamic equilibrium."

What is the justification for such statements? What researches have been stimulated or assisted by the concept of " the complex organism " *as such?* Professor Phillips seems to have in mind co-operative work in which plant and animal ecologists take part. But nobody denies the necessity for investigation of *all* the components of the ecosystem and of the ways in which they interact to bring about approximation to dynamic equilibrium. That is the prime task of the ecology of the future.

We cannot escape the conclusion that the supposed methodological value of the concept of the " complex organism," contrasted with the value of succession, development, climax and ecosystem, is a false value, and can only mislead. And it is false because it is based either on illegitimate extension of the biological concept of organism [5] (Clements) or on a confusion between the biological and " organicist " uses of the word (Phillips).

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[5] Clements is quoted as saying that biologists present at the evolution of multicellular from unicellular organisms would have denied that they *were* organisms, because they were *different*. Perhaps; but from our superior vantage point we can assert with perfect confidence that the so-called " complex organism " is vastly *more* different from either multicellular or unicellular organisms than they are from one another.

CONCLUSIONS

*Succession* is a continuous process of change in vegetation which can be separated into a series of phases. When the dominating factors of change depend directly on the activities of the plants themselves (autogenic factors) the succession is *autogenic:* when the dominating factors are external to the plants (allogenic factors) it is *allogenic*. The successions (priseres) which lead from bare substrata to the highest types of vegetation actually present in a climatic region (progressive) are primarily autogenic. Those which lead away from these higher forms of vegetation (retrogressive) are largely allogenic, though both types of factor enter into all successions.

A *climax* is a relatively stable phase reached by successional change. Change may still be proceeding within a climax, but if it is too slow to appreciate or too small to affect the general nature of the vegetation, the apparently stable phase must still be called a climax. The highest types of vegetation characteristic of a climatic region and limited only by climate form the *climatic climax*. Other climaxes may be determined by other factors such as certain soil types, grazing animals, fire and the like.

The term *development* may be applied, as in ordinary speech, to the appearance of any well-defined vegetational entity; but the term is more strictly applied to the autogenic successions leading to climaxes, which have several features in common with the development of organisms. Such climaxes may be considered as *quasi-organisms*.

The concept of the " biotic community " is unnatural because animals and plants are too different in nature to be considered as members of the same community. The whole complex of organisms present in an ecological unit may be called the *biome*.

The concept of the " complex organism " as applied to the biome is objectionable both because the term is already in common use for an individual higher animal or plant, and because the biome is not an organism except in the sense in which inorganic systems are organisms.

The fundamental concept appropriate to the biome considered together with all the effective inorganic factors of its environment is the *ecosystem,* which is a particular category among the physical systems that make up the universe. In an ecosystem the organisms and the inorganic factors alike are *components* which are in relatively stable dynamic equilibrium. Succession and development are instances of the universal processes tending towards the creation of such equilibrated systems.

From the standpoint of vegetation biotic factors, in the sense of decisive influences of animal action, are a legitimate and useful conception. Of these biotic factors heavy and continuous grazing which changes and stabilises the vegetation is an outstanding example.

The supposed methodological value of the ideas of the biotic community and the complex organism is illusory, unlike the values of plant community,

succession, development, climax and ecosystem, the concepts of which form the essential framework into which detailed studies of successional processes must be fitted.

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dans l'immense domaine de toute la moitié occidentale du Pacifique inter-
tropical, polynésien, jusqu'au delà du 180° Long. où commencera, pour nous,
le Pacifique oriental.[4]

Le Pacifique tempéré-nord est sillonné par les itinéraires des navires
ayant pour têtes de lignes Yokohama, Victoria (Vancouver), San Francisco
et Honolulu (Iles Sandwich).

Bien rares, toutefois, sont les documents planktoniques recueillis jusqu'ici
dans cette région.

Le séjour du Challenger à Honolulu (27 juillet-11 août 1875) n'a pas
laissé, à cet égard, plus de traces positives que son séjour ultérieur à Tahiti
(18 septembre-3 octobre) pendant la traversée N.S. du Pacifique intertro-
pical le long du 150° Long. W.

Au delà du tropique du Cancer, vers le Nord, nous ne pouvons guère
mentionner que deux récoltes sans individualité floristique bien tranchée,
faites en plein océan, par Schröter et Pernod du 18 au 21 septembre 1898
entre San Francisco et Honolulu (V. Br. Schröder 1906 p. 339).

Les publications de Lemmermann (1899 et 1905) sont les seules qui nous
renseignent, dans une certaine mesure, sur le phytoplankton des îles Sand-
wich, donc à la hauteur du tropique du Cancer entre 150° et 170° Long. W.
Parmi les Péridiniens récoltés par le Dr Schauinsland (septembre-octobre
1896) nous remarquons: *Pyrocystis pseudonoctiluca, P. fusiformis, Ceratium
furca, C. gibberum* var. *contortum* ( = *C. saltans* ?), *C. gravidum, C. macroceros,
Ceratocorys horrida* var. *longicornis, Phalacroma mitra, Amphisolenia palmata,
A. schauinslandii, Ornithocercus quadratus.*

Les Diatomées sont relativement rares, à l'exception de quelques
*Rhizosolenia (Rh. semispina, Rh. acuminata, Rh. styliformis)* et de *Hemiaulus
delicatulus.*

Le caractère néritique s'accentue dans les récoltes faites en juin 1896 au
"Pearl Harbour" de l'île Oahu (Honolulu) où plusieurs *Chaetoceros (Ch.
diversum, Ch. laciniosum, Ch. peruvianum)* sont accompagnés par *Skeleto-
nema costatum, Hemiaulus hauckii* et divers *Nitzschia.*

Le Mémoire de 1899 contient aussi l'analyse de quelques récoltes faites
par A. Barber. Les plus intéressantes proviennent des eaux chaudes du
contre-courant pacifique équatorial, vers 6° Lat. N. et 111°–112° Long. W.,
avec *Ceratium macroceros, C. furca, C. extensum, C. digitatum, Ceratocorys
armata, C. horrida* var. *longicornis, Amphisolenia palmata, A. thrinax* ——
*Planktoniella sol, Rhizosolenia semispina, Rh. acuminata, Bacteriastrum
elongatum, Chaetoceros lorenzianum.*

Nous atteignons ainsi le vaste champ de travail où s'exerce, depuis le
commencement du siècle, une activité américaine particulièrement féconde,
sous la puissante impulsion de Ch. A. Kofoid.

Les matériaux élaborés avec une continuité, une ampleur et un art

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[4] Au sujet de la croisière de l'Omaha, de la marine de guerre américaine, voir p. 308 en
note.

inégalables par l'éminent professeur de l'Université de Californie proviennent, comme on sait, de deux sources principales: 1) Récoltes locales, effectuées à l'aide de l'outillage des laboratoires de biologie marine de San Pedro (1901–1903), de San Diego (1904–1907) et finalement de La Jolla (Scripps Institution) depuis 1907.    2) Echantillons de plankton recueillis pendant l'importante croisière de l'Albatross, dirigée par A. Agassis, d'octobre 1904 à mars 1905; le trajet de l'Albatross à travers le Pacifique a dessiné, entre les tropiques un immense **W** dont les principaux repères furent Callao (Pérou), île de Pâques (Easter I.), les Galapagos, Manga Reva (île Gambier) et Acapulco (Mexique).

Tous les spécialistes connaissent et admirent les Monographies magistrales consacrées aux Dinophysidés, aux Gymnodiniens, aux *Heterodinium*, à quelques autres genres par Kofoid et ses collaborateurs.

Malheureusement l'œuvre est loin d'être achevée et nous ne possédons encore, pour le Pacifique intertropical, aucune vue d'ensemble relative à des genres tels que *Ceratium*, *Peridinium*, etc. aussi importants, quantitativement, que diversifiés spécifiquement.

D'autre part, Kofoid et ses collaborateurs ont considéré la question sous un point de vue plutôt zoologique, et nous ne savons encore rien de précis concernant l'existence et la nature des diatomées pélagiques dans les récoltes de la croisière orientale de l'Albatross.

On ne peut, dans ces circonstances, que se réjouir de l'heureuse initiative prise par la "Scripps Institution of oceanography," qui a chargé (en 1917) W. E. Allen d'organiser une étude méthodique continue du phytoplankton le long des côtes américaines du Pacifique oriental.

Le matériel étudié dans les laboratoires de la Scripps Institution a été toujours récolté de la même manière, depuis 1919, selon les directives de W. E. Allen, et analysé statistiquement par lui-même ou sous son contrôle.

D'après sa provenance, ce matériel peut se répartir en deux catégories: 1) Récoltes faites en plein océan, loin des côtes, échappant sans doute plus ou moins totalement aux influences continentales: récoltes très pauvres en général; il a été déjà question, brièvement, de la plus importante d'entre elles (Voir p. 308).    2) Récoltes effectuées dans les eaux littorales, le long ou assez près des rivages, c'est à dire dans une zone maritime plus ou moins soumise à des influences continentales.

L'enquête poursuivie par W. E. Allen et ses collaborateurs, jusqu'à ce jour, s'étend des côtes du Pérou (Callao) à l'Alaska et aux îles Aléoutiennes, c'est à dire depuis les côtes du Pacifique sud-tropical jusqu'aux latitudes boréales extrêmes (60° N).

Les résultats acquis ne nous concernent évidemment pas tous au même degré et nous pouvons, dès maintenant, faire abstraction des observations réalisées au delà du 45e parallèle N. et dans les eaux canadiennes.

Les très nombreuses opérations de pêche effectuées le long des côtes de l'Amérique centrale (depuis Panama), du Mexique et de la Californie, ont

donné lieu à la publication de divers "Rapports" dont les plus généraux sont celui de W. E. Allen lui-même (novembre 1928) et celui de Miss Easter Cupp (juillet 1930).

Ils peuvent être complétés, dans une certaine mesure, par les détails relatifs à la zone Panama-Callao, contenus dans la relation de la croisière du yacht Ohio, récoltes faites par E. W. Scripps, propriétaire du navire, en janvier-février 1924 et analysées par W. E. Allen (1925).

D'après Allen toutes les formes dominantes (diatomées) de ce plankton paraissent les mêmes que celles trouvées auprès de la côte californienne.

La plus récente Note de Miss Cupp (janvier 1934) nous inquiète encore un peu par ses *Bacteriastrum* species, *Chaetoceros* species, *Coscinodiscus* species, *Rhizosolenia* species.

De plus la liste de ses espèces dominantes ne comprend pas *Asterionella japonica, Eucampia zodiacus, Hemiaulus hauckii, Chaetoceros socialis*, etc., abondants ou prépondérants dans d'autres pêches.

Les Dinoflagellates n'occupent, dans cette intéressante série de Mémoires, qu'une place minime, en rapport avec leur rôle pratiquement négligeable comme éléments constitutifs de l'"ocean pasturage."

*Prorocentrum micans*, provocateur occasionnel d'eau rouge, *Ceratium tripos* (??), *C. furca, C. fusus, Peridinium divergens* (??), *P. depressum, Gonyaulax polyedra, Dinophysis caudata*, sont à peu près les seuls capables d'atteindre, çà et là, une proportion numérique assez forte pour jouer un rôle sensible comme "primary food" océanique.

En résumé, l'ensemble de ces recherches montrent que le gros du phytoplankton néritique des côtes américaines du Pacifique est constitué par un petit nombre d'espèces banales, cosmopolites, plus ou moins répandues dans toutes les mers.

Or cela ne saurait suffire pour caractériser la véritable physionomie biologique du vaste Pacifique.

L'océan est un désert, c'est entendu; [5] mais dans l'immensité de ce désert vit une élite dont les représentants, épars, méritent d'autant plus d'être recherchés et reconnus, en raison de leur rareté et de leur dispersion.

Une partie, trop faible encore, de ce monde du désert nous a été révélée par les admirables descriptions de Ch. A. Kofoid et de ses collaborateurs.

Mais, comme dit fort justement W. E. Allen (1927, "it will take a vastly greater amount of work than has yet been done to give a satisfactory understanding of life in ocean waters far from shore."

Une intéressante contribution à cette œuvre de découverte a été récemment fournie par un Français, Alain Gerbault, le "navigateur solitaire"; pendant une de ses randonnées transpacifiques, Gerbault a fait, du 14 novembre au 13 décembre 1933, une série de récoltes s'échelonnant, presque en droite ligne entre les Galapagos et les Marquises (Marquesas Islands) et coupant, par conséquent, l'itinéraire de l'Albatross (1905) entre les stations 4535 et 4537 de la carte de Kofoid (February, 1907).

[5] Cf. Pavillard, 1925.

Ce matériel dont j'ai donné l'analyse dans le Bulletin de l'Institut océanographique (Monaco, 1935), présente, dans la plupart des stations un mélange où les Diatomées l'emportent par le nombre des individus et les Péridiniens par le nombre des espèces.

La population diatomique est caractérisée par l'absence presque totale des *Chaetoceros* et, d'une manière générale, de toute la florule néritique, remplacée par des espèces nettement pélagiques:

*Hemidiscus cuneiformis, Coscinodiscus nodulifer, C. radiatus, Asteromphalus elegans, A. heptactis, Planktoniella sol* (très abondant), *Pseudoeunotia doliolus,* dont les curieuses colonies en manchon cylindrique sont souvent fixées, à l'état d'épiphytes, sur les thèques du *Tintinnus apertus* (Kofoid-Campbell 1929).

Le groupe des Péridiniens, très diversifié compte, dans l'ensemble, plus de 90 espèces dominées par *Ceratium breve, C. deflexum, Peridinium longipes,* mais où figurent aussi quelques-unes des individualités les plus caractéristiques du plankton pélagique thermophile:

*Ceratium gravidum* (var. *angustum* et var. *latum*), *C. reflexum, C. dens, C. incisum, C. geniculatum, C. praelongum, Histioneis biremis, H. gubernans, H. mitchellana, Ornithocercus carolinae, Gonyaulax glyptorhynchus, G. ceratocoroides, Podolampas reticulata, Cladopyxis brachiolata* ( = *Acanthodinium caryophyllum* Kofoid).

Ces constations faites sur une douzaine de récoltes effectuées en un mois, permettent de prévoir la récompense promise aux efforts futurs lorsque sera, quelque jour, organisée l'exploration méthodique du Pacifique.

MONTPELLIER, 10 MARS, 1935.

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# THE RELATION OF GENERAL ECOLOGY TO HUMAN ECOLOGY [1]

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## THE GENERAL BACKGROUND

"Our coordinated knowledge which in the general sense of the term is Science, is formed by the meeting of two orders of experience. One order is constituted by the direct, immediate discriminations of particular observations. The other order is constituted by our general way of conceiving the Universe. They will be called, the Observational Order, and the Conceptual Order. The first point to remember is that the observational order is invariably interpreted in terms of the concepts supplied by the conceptual order. . . . We inherit an observational order, namely types of things which we do in fact discriminate; and we inherit a conceptual order, namely a rough system of ideas in terms of which we do in fact, interpret." (Alfred N. Whitehead. "Adventures of Ideas," p. 198. 1933.)

It is generally difficult to estimate relative values, and yet the effort must be made if science is to advance. The progress made in ecology, both plant and animal, during the past third of a century appears to be of epoch-making importance. This may not be evident at a glance, but there is considerable evidence which supports this opinion. The present paper is devoted primarily to discussion of the general methods of studying ecology.

Progress may be measured either by the acquisition of new observational facts, or by new ideas and generalizations, as Whitehead has indicated. In this connection let us recall the work of Darwin and Wallace. In spite of the vast number of facts discovered by these great naturalists, their greatest contribution was their method of *interpreting the facts from a genetic or process viewpoint.* By means of their critical and analytical studies, supplemented by their constructive imagination, they were able to make such important and original hypotheses that their generalizations have dominated the minds of the scientific world for 75 years. It is thus seen that scientific advances depend upon the discovery of *objective* facts and *subjective* concepts, and that both kinds of discoveries are of the utmost importance; and finally we should bear in mind the fact that nothing is gained by belittling or minimizing the influence of either.

Taxonomic, floral and faunal methods of study have developed somewhat in advance of the ecological, and just as the older non-genetic taxonomy paved the way for the species problem and modern taxonomy based on

descent, so the older floral and faunal studies were transformed under the influence of the evolutionary concepts and thus they became increasingly genetic.   There also always remains in ecological studies a hereditary or genetic factor.   We should also recall that ecologic field study and genetic faunal studies were a vital influence in the greatest discoveries made by both Darwin and Wallace.

There has developed during this recent period very great progress in the physical and chemical means of analyzing biological problems.   This was no doubt closely related to the refinements of our scientific and technical industrial advances.   This has been the period during which microscopic technique dominated our laboratories to such a degree that the conception of the life of the plant and animal as a whole was almost, if not completely lost sight of, and direct contact with these organisms in their field relations was sadly neglected.   During this period the laboratory training of the urban universities and colleges tended generally to ignore the relation of living plants and animals to natural conditions.   Most of the students at the sea-side laboratories retained this indoor attitude.   Students with such a background were generally not interested in outdoor studies, live organisms, or ecological research, and often they found it impossible to adapt themselves either to the theoretical aspects or to ecological field study.   Many of the leading colleges and universities even today remain in this stage of development, almost harking back to the days when Latin and Greek were the universal college entrance requirements, and illustrating what the sociologists call "cultural lag," and the ecologists call "relic" conditions.

Another dominating influence during this period has been the rediscovery of Mendel's study of heredity.   Following this came the work of Bateson, De Vries, Morgan and others, initiating one of the most rapid advances in the history of biology.   The results of this brilliant period have so overshadowed many other lines of study as to obscure the perspective, and even now it is difficult to evaluate thoroughly its contribution to general biology and to ecology.   However, some students like Jennings ('24, '25, '30), express certain opinions that are quite significant from an ecological point of view.   Thus this author states ('24, p. 225):" Organisms are like other objects in this respect; what they do or become depends both on what they are made of, and on the conditions surrounding them.   The dependence on what they are originally made of we call heredity.   But no single thing that the organism does depends alone on heredity or alone on environment; always both have to be taken into account. . . . (Page 233.)   But the fruit flies in the laboratory usually live in moist air; this inheritance appears under those conditions.   If they are hatched and live under dry conditions the abnormality doesn't appear—even in those daughters which indubitably inherit it.   Clearly, it is not necessary to have a characteristic merely because one inherits it.   Or more properly, characteristics are not inherited at all; what one inherits is certain material that under certain conditions

will produce a particular characteristic; if those conditions are not supplied some other characteristic is produced."

Such statements as the above indicate that the discoveries and the literature of ecological significance are by no means limited to the journals or serials devoted to ecology, and show that the ecologist must forage over the whole field of biology and the allied sciences for his significant facts and inferences, and much of value will be found in rather unexpected places. It is of interest to observe that some students of heredity apparently do not see the ecological and environmental significance of their own results.

Our knowledge of the general physiology of plants and animals, including their behavior and habits, has progressed as never before. The refinements of physics and chemistry have revolutionized the general conceptions of physiology, and as a result both plant and animal physiology and behavior have been largely rewritten. Our understanding of the functions of plants and animals as individual entities or unit systems has advanced to a higher recognized standing, and is coming to be more clearly accepted as subjects worthy of serious study. Individuality is coming to be considered as both a condition and a product of creative ability. The community behavior of plants and animals will probably next receive a clearer recognition, and appropriate study, and this advance will pave the way for a better understanding of human social relations.

Our knowledge of the gross physical environment has also advanced by great strides. The progress in dynamic climatology, physiography, regional geography and exploration, geological history, human geography, as well as in the dynamic study of economics and sociology, have all contributed generalizations and facts that are of great value for ecological advance. Modern geography has a very distinctly ecological slant, and it is no longer a rare event to find the word ecology in geographic, economic and sociological literature.

We thus see that the recent important advances in ecology have been along descriptive, dynamic, functional, experimental and genetic lines, and that not only has there been an extensive accumulation of new facts, but also as well, a considerable increase in new generalizations, and that much definite integration has taken place between the allied sciences. The newer studies of heredity have made important contributions to the relative influence and meaning of heredity and the environment; the advances in physiology and behavior, as well as anatomical progress, have also contributed to this general movement. The advances in taxonomy have promoted both floral and faunal studies and have given them a richer genetic interpretation, and upon such a broad foundation modern plant and animal ecology has expanded, bringing out the deeper significance of biotic communities, which suggests that such studies will periodically contribute much toward a better foundation for an understanding of human economics, and social and governmental problems.

## DYNAMIC AND PROCESS VIEWPOINT

"Constructive and destructive agencies can be recognized only when the phenomena are made the basis of the scheme. Processes are merely operative. If coupled with the products at all, in classification, all must be regarded as formative or constructive. The product's destruction, its loss of identity, is wholly immaterial. The action of agencies is merely to produce constant change. A truly genetic scheme for the classification of natural phenomena thus always has prominently presented its underlying principle of cause and effect. All products must find accurate expression in terms of the agencies." (Keyes. 1898, p. 812.)

"But in the development of modern physics and chemistry, the same thing is now happening to the physicists. Regarded from this standpoint, it is no longer merely living beings, but the whole of nature which has become an architectonic structure, the richer and the more complex the more it is investigated by science. It is science which has created our conception of this architecture, and its extension from the living into the inorganic world makes the whole structure not less, but still more wonderful. From this point of view, the word organization is a biological expression for the same thing as is known to physics and chemistry as a system." (Johan Hjort, "The Unity of Science," pp. 164–165.)

The ramifications of ecological relations are so varied that a considerable number of general ideas adapted from the allied sciences are constantly being developed and should be utilized. To mention them would be to summarize the status of the useful generalizations in the related sciences. However, when we consider the present status of ecology some of these generalizations are apparently of more immediate interest and value than others, and therefore only a few will be selected for brief mention.

The dynamic and process point of view is a generalization that has been of relatively slow growth. It has been spreading gradually in the biological sciences and has made rather rapid progress in some aspects of ecology. I have discussed various phases of this subject in relation to the dynamics of habitats and migrations, and to biotic or climax centers rather frequently (Adams '01, '02, '02a, '04, '05, '06, '08, '09; '13, '15, '15a, '15b, '18–'19), and important revisions and qualifications are now much needed because of recent advances (cf. Lotka '25). Cooper ('26) has discussed certain dynamic aspects of plant ecology more fully than other authors, and special attention is called to his important paper. Of course a large number of students have emphasized various phases of this subject, but in general the clearest expression of these general ideas have come from the students of the physical and earth sciences (Keyes, '98; Van Hise, '04), and more recently from the ecologists, physiologists, and others. Some physiologists have accepted the ecological ideas and terminology of dominance, zonation and gradients. Fundamentally this means that we are dealing with the causes and laws of change in the environment and in organisms, distinguishing the energies involved, the activity of the *agents* or the *systems*, their dynamic status, their relative optima, limiting factors, and the orderly sequence or succession of their internal and external changes (Adams, '13, '15, '18–'19).

It should be evident that field work as well as experimental studies may be made more fruitful by the use of such ideas. These ideas should be considered in the same light as other tools, both those of the field and of the laboratory, for they are in reality mental tools. Like other tools they may become dulled, useless or outgrown, and should then be discarded. Skill in the use of ideas varies also as does skill with other tools; some have dexterity, some mechanical skill, others have theoretical skill, but rarely is one person gifted with the use of all. These tools, like the student himself, have their limitations, and the practical problem is to make the best use of all facilities that are available under the circumstances.

In cases where the causes are obscure, attention should be concentrated on the activity of the agent or the system, its processes and cycles of activity should be determined, as well as its dynamic status (Adams, '18–'19, pp. 470–477, and "Reports of the Conferences on Cycles," Carnegie Inst. of Washington, 1929). As I have said elsewhere (Adams, '18–'19, p. 471), "The dynamic status means the condition of a unit or system with regard to its degree of relative equilibrium. The cycle of change may be considered to begin at any point. I have taken as the initial stage of the cycle the condition of stress and pressure and have indicated how this condition tends to change in response to pressure, bringing about the process of adjustment to strain, and leading to the condition of adjustment to strain, or that of relative equilibrium. The activity of the agent produces the condition of stress, the process of adjustment to the strain follows, and this leads to the product—the establishment of the condition of adjustment or of relative equilibrium." These ideas apply to the life cycle, and to development and possibly to the race. In the light of recent interpretation of Jennings ('24, '25, '30) it seems that Vernon's law (Vernon, '03, p. 199) with regard to the progressively diminishing influence of the environment after the impregnation of the egg, will have to be modified.

The activities of plants and animals as agents or systems, because of their active lives, are continually colliding with the environment or are bombarded by the environment. This is the basis for the friction and interaction between the organism and the environment. Fortunately, in recent years a comprehensive study has been made of several of these physical conceptions by Lotka ('25) as well as by others, and special attention is called to his volume, because it contains valuable discussions and criticisms of the earlier work, including equilibria, the principle of Le Chatelier, Bancroft's law (Bancroft, '11), and related ideas. His discussion of the applications and limitations of physical changes, in relation to biological problems, is quite illuminating. (See also Pike, '23; Wardlaw, '32.) Today there is urgent need for a similar evaluation of the so-called "optimum," and "limiting factors," including Liebig's law of the minimum and its various modifications, and the law of diminishing returns (Spillman and Lang, '24; Black, pp. 635–644, in Rice, '31; and Willcox, '30). See also Blackman,

'05, '08; Blackman and Smith, '11; Adams, '04, '15, '18–'19; Nichols, '17; Hooker '17, '19; Chapman, '31; and Allen, '34.

Many of the problems of the ecologist have not yet reached the stage that permits precise physical and mathematical formulation, and therefore useful generalizations are welcome which are less precise, but no less serviceable. It is desirable that whenever possible these formulations should be given the process and dynamic form of expression and sequence because of its emphasis on causal relations.

In dealing with the gross physical environment greater dependence is placed upon physical laws, because they operate without the complexity that is involved when organisms are included. The dynamic status of organic systems, their cycles of action, and their trends in relation to other organisms are of the greatest interest and importance. Thus climate, topography and geological influences all contribute environmental successions. Some of the main dynamic generalizations of the physical world apparently apply also to plant and animal communities in varying degrees, and are very suggestive as well in connection with human economic and social problems.

That the organic world does not expand wholly at random, suggests that there are both internal and external factors that limit it under existing conditions. Some of the internal factors are clearly those imposed by the hereditary history; and these are possibly restricted by both physical and chemical limitations and affinities. The external limiting factors are likewise varied and complex, and many efforts have been made to formulate the relations of these two major systems and their laws of change or orderly sequence.

The dynamic and process viewpoint has therefore already made available a considerable variety of guiding ideas and working hypotheses for ecological work, but one must not assume that these are of equal value. There are also great differences of opinion among scientists regarding both their basal assumptions and their method of application, so that it is very desirable for each one to know definitely on what hypothesis his own work is based and to recognize that used by others.

## PLANT AND ANIMAL ECOLOGY

"To study life we must consider three things:
*first*, the orderly sequence of external nature;
*second*, the living organism and the changes which take place in it; and,
*third*, that continuous adjustment between the two sets of phenomena which constitutes life."

"The physical sciences deal with the external world, and in the laboratory we study the structure and activities of organisms by very similar methods; but if we stop there, neglecting the relation of the living being to its environment, our study is not biology or the science of life." William K. Brooks, "The Foundations of Zoology," 1915, p. 54.

"We are apt to contrast the extreme of instinct and intelligence to emphasize the blindness and inflexibility of the one and the consciousness and freedom of the other. It is like contrasting the extremes of light and dark and forgetting all the transitional degrees of twilight. . . . Instinct is blind; so is the highest human wisdom blind. The distinction is one of degree. There is no absolute blindness on the one side, and no absolute wisdom on the other." C. O. Whitman, 1899.

" It is essentially a recognition of the fundamental identity of the animal and human souls, the differences between which are regarded merely as differences of degree of development. This implies that intelligence is not exclusively human and that the animal mind is to be interpreted in the light of human psychology, a procedure which is, of course, open to the charge of anthropomorphism. But owing to the fact that all our science is necessarily anthropomorphic and that man himself is merely a highly developed animal and therefore could not if he would interpret other animals except in terms of himself, the charge can only mean that he continually runs the risk of attributing to animals a greater development of intelligence than they possess." William M. Wheeler, "On Instincts," Jour. Abnormal Psychology, Dec. 1920–March, 1921, p. 302.

The above quotation from Brooks shows a grasp of the process point of view that is not prevalent even today. We should not, read into this more than it meant to him, but that does not weaken its validity. To consider the orderly sequence of external nature means that the dynamic status of a system must be determined, its cycles of activity must be known, and its trends, succession or orderly sequence must be determined, and finally its relative dynamic equilibrium must also be established or anticipated. Until some progress has been made along these lines not much of scientific interpretation is to be expected. Fortunately, as has been indicated, much has already been done in the determination of physical dynamics. This is seen in the daily, seasonal and other cycles, which furnish an extensive background for dealing with climatic influences and other physical processes. The crustal movements of the earth and the erosion of the lands provide other series of orderly sequences, and furnish a background for the broad world relations that are of the utmost importance to the ecologist.

Turning to the orderly sequences within the plant and animal, first of all is the individual life cycle, which experience has shown to be of universal utility. And among the internal sequences are both those that are relatively stable and those that are relatively changeable. Among the conservative influences are heredity, certain forms of behavior and structure; and of the flexible kinds are many physiological responses, and also certain forms of behavior. Among plants and animals there are a large number of small cyclical, physiological and other rhythms that are available for study by this method. A culmination or extension of the life cycle system may be seen in certain groups of "social" insects, such as bees and ants, which are the outgrowth of a parental relation.

In addition to the individual life cycle there are those organisms that

are bound together by common racial descent, and thus form a taxonomic unit, and have a cycle of much longer duration than that of the individual. This produces the racial sequence or cycle; and thus with the individual and the race the strictly hereditary organic series is complete.

The only remaining major series is the grouping of organisms into living communities and associations, including both the hereditary groups and those that live together in the same area or unit of environment. This therefore involves their relation to the "land" surface of the earth. Thus the individual, the racial aggregations and the community include all of the major series of the orderly sequences with which organisms are concerned, from the lowest to the highest in the scale of organic complexity. With these series viewed dynamically, as well as those of the physical environment, the study of the process of interaction between the organism and its environment follows naturally and thus completes this picture. This series includes all the conditions stated by Brooks, and in addition it provides a genetic explanation of the relation of organisms to their complete environment, as the culmination of ecological relations.

As has been said, in dealing with internal and external successions, it is desirable that we should constantly do our habitual thinking in dynamic terms, bearing clearly in mind the dynamic status of the system, its condition of stress, its process of adjustment, and its relative equilibrium developed by this process. This is an orderly sequence. Finally, it should be repeated that by applying as many of the appropriate dynamic principles as possible—including such generalizations as the principle of Le Chatelier, the modified Bancroft's, Vernon's and Liebig's laws, the idea of a relative optimum, limiting factors, law of diminishing returns, the modifiability of behavior, and all that is *implied* in ecological successions (dominance, climaxes, etc.)—it is seen that a considerable variety of generalizations are now available for use. There are, of course, other principles and ideas that should receive adequate attention, and be brought into this field for discussion, evaluation and constant revision.

An important factor in ecological succession is the changing rate or flow of the population elements in the successive communities. As a rule, in a new unoccupied habitat the pioneers are few in number, but in time other organisms arrive, and as the population grows the relative proportions of the organisms are under constant changes in both numbers and kinds, as the competitive process advances toward the relative dynamic equilibrium of the climax association. This is the result of the balancing of all the biotic influences in relation to the environment. It appears to be a self-limiting series or system, and the relative stability of the climax is probably only apparent. In some conditions the climax association tends to include or retain numerous individuals of a few kinds; but in others a relatively large number of kinds of individuals persist. The fluctuations of these populations during succession is a very complex problem. Efforts have been

made to apply the early quantitative methods developed in the study of plankton to other plant and animal community populations; notably by Clements and others, and we may expect an extension of such methods. Others have attempted to apply the general biological results of population studies to the competition among populations, as has been done by Lotka ('25), Chapman ('31), Volterra (See Chapman, '31, pp. 409–448) and Gause ('34, see particularly p. 10). This involves also a study of the influence of limiting factors.

The world-wide applications of these numerous generalizations should give proper consideration to the diversities of plants and animals in the varied habitats and biotic regions of the world, and relate them not only to their environmental history but, also to their ancestral history, which has resulted in that taxonomic diversity which is seen in the biota, and their mosaic distribution over the face of the earth both in floral and faunal areas as well as in social communities or centers. What we see today is a complex mosaic pattern, due to both of these biological influences and to the varied physical history of the different parts of the world. This complexity is the result of the conservative effects of racial history due to heredity, and the constant battle of adjustment and transformation that has gone on between the biota and the environmental history through the ages.

Within the field of plant ecology the works of Warming ('09), Cowles ('99, '11), Clements ('01, '05, '16, '28), and Tansley ('20) are outstanding, and there has been no equally extensive or comprehensive work in the more complex field of modern animal ecology. The valuable earlier work by Semper and de Varigny antedated the modern movement, and was not in line with much of the later major developments, with the possible exception of the valuable work of Child ('24) and Allee ('31) on the physiology and "hygiene" of aggregations. The later and most comprehensive works on the communities of animals was by Ruthven and others ('06), Adams and others ('09), Adams ('08, '09, '09a, '09b, '13, '15, '15a, '15b), Shelford ('13) and Chapman ('31), their students and others. Of work in the Old World mention should be made of that by Kashkarov ('33) and Elton ('27).

The ecology of the American fresh water biota, particularly that of lakes, has been given extensive study. Considerable attention has been given to their physical and chemical conditions and to the quantitative study of their plankton. Streams have been much neglected, with the notable exception of the Illinois River. Plankton studies, both fresh water and marine, early became quantitative, but did not adopt the ecological ideas of the period, and have remained relatively static; later they became more physiological, but did not become thoroughly dynamic, and recently have not made great progress from the community standpoint.

The Danish fresh water studies have often had a more modern standpoint, no doubt due to the relatively advanced position of ecology in Denmark. The most illuminating work on marine animal ecology has been that

in Danish waters, and the best general statement of shore conditions is by Flattely and Walton ('22). We have no corresponding marine work in America, in spite of the early example by Verrill, and the many years of active work by several marine biological institutions.

The development of the emotions and of greater intelligence in the higher animals and man introduces certain qualitative differences in responses that influence all ecological relations. There is much in common between the sessile animals of the sea and plants (Shelford, '14), so much so that for a long time there was much confusion as to their affinities and reactions. Even among free-living animals and plants there are innumerable degrees of freedom. Many animals are relatively sedentary and their lives are confined to a small area of land or water, and even animals of considerable intelligence are often similarly limited, while still others wander extensively or make prolonged migrations, as the birds, bats and whales. The relative freedom of motion in animals has possibly led to an overestimate of their freedom and to the neglect of those limitations of the environment and of behavior that together restrain them. Much has been made of physical and geographic barriers, and there is no doubt as to their influence, but the physiological and mental limitations have not been as fully studied (cf. Rabaud, '28; Heape, '31). It is only in recent years that the regional spacing of breeding birds has received independent recognition and study (cf. Adams, '08, pp. 140–42; Howard, '20, '29; Mousley', 19, and Saunders, '29), not only for its influence upon breeding habits but also on account of its influence upon succession. That birds which nest in large colonies on the shores space themselves has long been observed, but that a similar but larger unit of spacing applied to the majority of birds during their breeding season was much slower in gaining adequate recognition. Many mammals are similarly limited, such as rabbits, deer and those which are closely tied to a burrow or a den. The behavior of animals is thus seen to limit their freedom of action and as a result it orients them in space; and combined with the physical barriers it indicates that these influences are important controlling factors in their successional relations. Many kinds of invertebrates show similar local limitations. These influences determine the choice or selection of a habitat when an animal has a chance to exercise a preference. The behavior of animals, as limited by their physiology, emotions, instincts and intelligence, is thus seen to be of the greatest importance in orienting them and the role which they play in any given animal and plant community, or as well in understanding their successional relations.

Considerable advances have been made in recent years in the study of animal behavior, and the summaries and discussions by Jennings, Holmes ('11), Thorndike ('11), Washburn ('26), Watson ('19), Wheeler ('10, '23, '28), Holt ('15, '31), Tolman ('32) and many others indicate the status of this field.

Certain authors, as Wheeler ('10, '23, '28), Alverdes ('27) and others

have given much attention to the relation of animals to one another from what has been called a "social" point of view, as in the case of ants and other "social" insects, but this is not the "social community" of the plant and animal ecologists. As previously mentioned Allee ('31) and Child ('24) have extended and elaborated physiological and ecological ideas of animal aggregates, and have indicated some of their applications to human social relations.

I am inclined to the view that animal and human sociology includes all intimate physiological and "sanitary" interrelations between the individual members of ant and other "social" insects, and that these relations are to be included in the larger synthesis of the ecological community to which they belong; and that it is primarily to the responses of this more comprehensive unit that we must look for the greatest illumination bearing on the broad human social relations. In other words, human social communities are not solely the outgrowth or blossoming of the physiological, aggregational or parental relations of animals, but involve as well an added factor or influence provided by the ecological social community.

In looking forward to the transition from the ecology of the lower animal to human social ecology it is very important to recall Wheeler's ('21, p. 318) remark that "the subconscious *is* the animal mind." It seems rather strange that during the modern revival of active interest in animal behavior, intelligence seems to have attracted the most attention, while it would seem that the most revealing behavior would come from a study of animal emotions (cf. several papers by Craig, '09); and it is probable that the study of emotions will in the near future throw the most light upon human behavior and social conditions. It appears that the work of the psychoanalyests has helped to bridge this gap in part. The results of their studies, as interpreted by Holt ('15, '31), and by the leading English plant ecologist Tansley ('20a), will prove particularly valuable in studying the transition from animal to human social behavior.

As we advance from the individual to the social community we have an ascending series of systems which become increasingly complex, and whose *interaction* and *integration* are of paramount importance (cf. Adams, '18–'19). Integration extends through all of these series of systems, and its processes include all the activities in response to the environment.

In concluding the sketch of this phase, mention is made of certain generalizations that have been developed as the outgrowth of the study of the succession of plant and animal communities, because they involve ultimately the summation of all ecological relations, individual, aggregate and community. Warming ('09, p. 356) summarized his views on plant successions, indicating initial, transitional and final communities. He showed that the pioneers that came from the vicinity were those with the best means of dispersal, and that there was the precedence of the light requiring trees over the shade enduring kinds. Cowles ('11) indicated the

next important step in his recognition of the climax as a stage of relative equilibrium. Clements ('04, pp. 133–136; '05, pp. 264–267) early summarized his views on the "laws of succession," and certain phases of animal succession were summarized by me (Adams '08, pp. 125–128). The next step is the application and extension of these general ideas to the distinctly human aspects of the general problem.

## SOME PHASES OF HUMAN ECOLOGY

"An important distinction needs to be made if there are to be social sciences differentiated from psychology. In this volume, the distinction is based upon functional groups, as distinguished from genetic groups. All behavior has social implications; the behavior with which this volume is concerned is explicit. The functional group (cooperative association) exhibits explicit social behavior; the genetic group (family) exhibits implicit social behavior. Within the family, behavior is social, whereas within the functional group, behavior becomes social by virtue of interests and purposes. The older sociology regarded the social process as a relation between individuals and hence social theory revolved about this relation. The present thesis is that a pragmatic sociology must regard the social process as a relation between groups." (Lindeman, '24, p. 354.)

"Economics, therefore, is merely Human Ecology, it is the narrow and special study of the ecology of the very extraordinary community in which we live. It might have been a better and brighter science if it had begun biologically. . . . And all we shall say will be based on general ecology. Man is so peculiar a creature that a really satisfactory treatment of the science of work and wealth demands a companion work upon the scale of this Science of Life. But here we hope to show that ecology lays the foundations for a modern, a biological and an entertaining treatment of what was once very properly known as the "dismal science" of economics." (Wells, Huxley, and Wells, '34, p. 962.)                          .

"From the biological point of view my Professors would be human ecologists; indeed Human Ecology would be a good alternative name for this new history as I conceive it. . . . They would be related to the older school of historians much as vegetable physiologists, ecologists and morphologists are related to the old plant-flattening, specimen-hunting, stamen-counting botanists. The end of all intelligent analysis is to clear the way for synthesis. The clearer their new history became the nearer they would be to efficient world-planning. . . . Sooner or later Human Ecology under some name or other, will win its way to academic recognition and to its proper place in general education—in America sooner than in Europe, I guess—but the old history made up of time-worn gossip and stale and falsified politics, is deeply embedded in literature and usage. The invasion of the field of history by the scientific spirit is belated and slow. . . . Just as the *Outline of History* was an experiment in analytical history, so this [Science of Life] was to be an experiment in synthetic, descriptive economics and politics. The exactest name for such a synthesis would be the 'Outline of Human Ecology.' But I did not call it that because the word Ecology was not yet widely understood." (H. G. Wells, "Experiment in Autobiography," 1934, pp. 552–553; 617.)

In the preceding section I have called attention to certain ideas and generalizations of general ecology. Several of these are known to be

broadly applicable to man because he is an animal, and as well because he is dependent upon the physical, plant and animal world as definitely as any other animal, although to a different degree.

In dealing primarily with the plant and animal world, we have seen that there are many generalizations and various points of view. Some of these are, in varying degrees, conflicting, antagonistic, and some are possibly contradictory. But if these ideas are critically and intelligently used even an erroneous conception may be so revised as to be a useful tool. In general, however, emphasis is placed upon the continuity of the processes and sequence of changes which are revealed in the sub-human biological world, rather than to emphasize their distinctness from the conditions found in human communities. The complexity involved in human affairs only emphasizes the need of keeping the problems in as simple terms as is possible.

The old relation of heredity and environment now becomes, in human affairs "nature" and "nurture," but there is nothing new about it. (Cf. Schwesinger, '33; Febvre, '25; Thomas, '25.) The hereditary diversity, and the blending of the races have given the racial variety which is bait for the politician, and the bane of the statesman, because between race and "culture" arise a vast number of world problems and conflicts.

The recognition of human ecology and the utilization of the definitely developed ecological ideas are of very recent development. The older authors recognized the general field but did not elaborate it. Several geographers, notably Huntington, in a series of books ('15, '27 and other volumes), have stressed the physical influence of the environment, particularly the climate, upon races and culture. Thomas ('25) has summarized the geographic influences on social relations. The racial aspects of Europe have been ably developed by Ripley ('15), while Taylor ('27), and Dixon ('23) have elaborated the origin and migration of the races of men, and finally an important critical study of the results of the mingling of races has been made by Hankins ('26). To the American the ecology of the Indian is of special importance, because of his role in the primeval environment, and this phase has been particularly well developed by Wissler ('26). He has shown very clearly the intimate relation of the natural resources, particularly the biological resources, to the culture of the Indians, and incidentally this also shows how much the Indian contributed to his dominant white successor, who has incorporated Indian corn, tobacco, cotton, potatoes, tomatoes and other plants, into his cultural system.

In recent years two outstanding treatises on biology have appeared by British authors, who have given unusual recognition to the relation of general ecology to human ecology; the first being by Wells, Huxley and Wells ('34) to which reference has been made in the quotation at the beginning of this section. The second is by Thomson and Geddes ('31) where the human social aspects are even more emphasized, but whose ecological standpoint is not so recent. In each work there was apparently a distinctly

social-minded author involved (H. G. Wells, and Geddes). The results of these discussions deserve widespread attention, as they are indicative of the newer outlook which is likely to become increasingly prevalent (cf. Tansley, '20).

It is significant to observe that as the application of the scientific methods to human social problems progresses, the methods of the natural history sciences and business technique are increasingly being applied to them. For this purpose the methods of the regional and ecological surveys are particularly appropriate and illuminating. These methods have been more prevalent in economic studies than in the social ones; no doubt because of the more frequent technical and scientific training of the students of economics. As examples of these recent social surveys, reference is made to the Lynds ('29) "Middletown," and Marshall's ('33) "Arctic Village." It could not be expected that the older social surveys would escape all the errors that were made by the older natural history surveys. They did not; but both have been greatly improved during the last 20 years in their technique and standardization, with the result that many significant comparisons are now possible. There is possibly too strong a tendency toward static business methods of study, rather than toward accumulating and interpretating the facts ecologically or functionally. Cross sections have their value, but the past and the future must receive attention in dealing with life relations, and provision should be made for this phase in the surveys or it will be lacking in the results. This means that specific efforts should be made to determine just what *processes*, *pressures* and *trends* are at work in any given condition or community. (Cf. Burgess, '16, on social surveys; Elmer, '17; Taylor, '19; and especially Allen and Harrison, '30). Another relation that is often neglected or slighted in social and economic surveys is the physical and biological foundation of the problem. Furthermore, if surveys are conducted from too narrow an angle they will defeat their own purpose.

Many years ago Geddes and Thomson at Edinburgh, Scotland, combined in their summer schools field courses and surveys of the biological and the *social* sciences (cf. Thomson and Geddes, '31, pp. 1384–1401), and they maintained a lifelong interest in such problems. This kind of combination has received relatively slight attention in this country. (Cf. Silloway, '20, and Brown, '20.)

Of the various techniques applicable to social problems, the methods of the physical sciences will prove the most valuable for the study of the physical aspects, of the economic and social environment; those of biology and of ecology for the primarily infra-human aspects, and to an important degree for the more primitive and backward human conditions, and possibly even for their emotions, habits and instincts. And finally, psychological and ecological methods must dominate the distinctly inter-human phases of the problem. To fuse the best features of all these general ideas and techniques

into a practical research program, and to apply them appropriately to any given problem, is one of the most important practical undertakings in human ecology. The sociologists have already made a "self survey" or intensive study of their own current methods, as actually employed by representative students in making important sociological contributions (Rice, '31), and ecologists might well follow their example. Sound procedures only will give dependable results, and as well develop an adequate perspective for their interpretation. At the same time the attempt to solve human ecological, economic and sociological problems solely on the psychological plane, without adequate recognition of the other ecological, biological and physical foundations, can give only incomplete and misleading results. We must never overlook the fact that human communities are never composed solely of one kind or species of animal. They are not "pure cultures," but are composed of the vegetation upon which they are directly or indirectly dependent, the human parasites, the commensals, and those animals exploited by man, as well as the human associates.

The processes by which human communities are integrated have been the object of much serious study. Thus Bagehot ('73) many years ago pointed out the value of discussion and competition, and many have discussed phases of this problem. In recent years outstanding insight in group activities and functions, group competition, adjustment and leadership, and particularly that of "participant" leadership, have been made by Lindeman ('24, '33) and Follett ('24). The technique that has been developed by these students will prove of value in other fields (cf. Hader and Lindeman, '33). The extension of these methods to the problems of government has been developed and emphasized by both Follett and Lindeman.

Other sociologists who have stressed the ecological approach to human sociology are McKenzie ('25, '27), Park and Burgess ('25) and Burgess ('27); Anderson and Lindeman ('28). Charles ('34) has stressed the ecological population problem. I am refraining from listing several prominent books on "social" psychology because these authors have apparently not yet appreciated that in addition to the individual and the aggregate aspects of ecology it is the social community aspect that is of supreme importance, in the study of human sociology, ecology and government. I am in hearty accord with Lindeman ('24, pp. 161–168) in this respect, as is indicated throughout this discussion.

As long as biology is taught and developed primarily from the individualistic, or solely aggregate standpoint, with slight or inadequate recognition of the social community aspect, the students of the allied sciences will continue to utilize and accept only the older concepts, and thus retard the integration of the biological and social sciences. Once more it seems necessary to state what has been stressed throughout this paper, that if emphasis is placed upon the process, dynamic and functional point of view,

some of this confusion, which is so clearly evident in dealing with human ecology, may be reduced or avoided. Advance in general ecology is now a limiting factor retarding the advance of human ecology. This entire discussion of human ecology has a direct application to ecologists themselves and to the advancement of ecology.

Let us now turn to the specific application of the process standpoint to general human ecology. From what source come the stresses or pressures in human relations? The answer is a simple one. Instead of universal uniformity in the physical features and the distribution of the natural resources of the earth, there is very great diversity and inequality. The complicated regional history, and the similar complexity among the plants and animal communities, all reflect this same variety, to which man himself is no exception. The results of this multiple diversity are far-reaching indeed, as these differences tend to produce relatively independent units or systems of action, and permit and reinforce the development of a certain amount of individuality and distinctness of both race and culture. Between these centers of individuality there develop pressure, competition, or friction of some degree (cf. Bancroft's law). Thus with physical, plant, animal and human diversity the stage is set for all degrees of pressure and stresses. Part of the pressure exerted upon man is a reflex, due to his own influence upon his environment. The broad features of this have seldom been studied in a thoroughly comprehensive manner. A classic in this field, which has never been superseded, is Marsh's "The Earth as Modified by Human Action" (1874), and the best allied recent work is by Ritchie, "The Influence of Man on the Animal Life of Scotland" (1920). In this early study Marsh (l.c. p. 297) pointed out that a fundamental contrast in land use is between the woodland and ploughland, a distinction of similar importance to the recognition of rural and urban lands. These distinctions furnish the bases for ecological units or entities. Land use also implies the mineral and biological resources in relation to man, which was developed by Van Hise (1910) in his "Conservation of Natural Resources in the United States." (See also for ecological aspects of this problem Clements, '16, '28, and Adams, '25, '25a, and '26). The interrelations that result from these basal relations are not only of primary ecological importance but are a practical problem of the first magnitude because of the need of maintaining a proper balance and adjustment between them. The processes of adjustment to pressure from these centers of stress give an unending series of changes. Not only do these processes operate in any given locality, but the physical conditions themselves change and even migrate, as do those of the biological and ecological environment. The rate of change varies greatly, some sectors moving more rapidly than others, among plants and animals as well as with man. And while all stages in the process of human social succession are not preserved, the broad outlines of social successions are even more completely known than are those of plants and animals to the ecologists.

The sociological succession of social relations thus opens up a large field of study.    The records of archeology and history contain a vast amount of data bearing on this subject, but the modern conceptions of ecological succession have not been extensively utilized in their interpretation, and very naturally, because of their imperfect organization of the subject by the ecologists themselves.    A fertile field awaits the attention of the student who will prepare himself for this next advance, and cultivate the neglected borderland between general ecology and human ecology.

Human ecology is not restricted solely to the past or to the present, it is also vitally concerned with the future.    It is the tradition of ecologists to endeavor to understand the present in terms of the past, and to regularly anticipate future successions and developments.    Likewise in the case of human ecology there is every reason to continue the same attitude.    There are many relatively persistent trends at the physical and biological levels, and even in the human successions as well, in spite of the frequent tendency to over-emphasize the uncertainties involved in anticipating the future. The present gap between the relatively advanced stage of several of the physical and biological sciences, and of the distinctly social sciences calls for special research before the next great advance can be made, and human ecology, broadly conceived, occupies a large part of that field.    General ecology has to contribute to this program confidence in the scientific method, a considerable number of working ideas and generalizations, and now we need students who will cultivate intensively this neglected field.

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# THE REPLACEABILITY OF ECOLOGICAL FACTORS AND THE LAW OF THE MINIMUM

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In vegetational research the investigation of the environment is a matter of primary importance as it comprises the totality of the acting factors. These climatic, edaphic, and biotic factors are very numerous. We would be able to form a correct concept if it were possible to grasp the total effect of all the factors involved. But this combined effect is of such a complex nature that we instinctively divide the problem and investigate each factor separately. Usually, however, it is impossible to investigate every factor, hence only those that are considered most important are undertaken.

Many concepts of vegetation have been based upon the " most important " factor. Among these are DeCandolle's (1874) concepts of megatherms, mesotherms, and microtherms based on temperature and his xerotherms based on moisture relations. There are also Warming's concepts in relation to moisture; his terms xerophyte, mesophyte, and hydrophyte are well known, as is .his concept of the halophyte based on salt-content relations. Generally it is undesirable to seek one important factor, because in the first place this factor may change locally, and besides, it is not at all probable that it is in itself really the most important; its significance is surpassed by a factor-complex composed of a group of several.

Liebig's well known and fundamental " Law of the Minimum," which he formulated for experimental cultures, has been generally recognized as applicable also to natural plant communities.[1]

A given factor can exert its effect only in the presence of and in conjunction with other factors. The factor which is present in minimum amount is then the limiting one. Thus a soil may be rich in nutrients but these substances are useless if the necessary moisture is lacking. And inversely with an abundance of water and sunshine plants cannot thrive without nutrients. In these cases we may consider the factor present in minimum amount the most important one. Here it may be this factor, there that one, elsewhere

[1] **H. Brockmann-Jerosch.** 1919. Baumgrenze und Klimacharakter. VIII + 255 pp. Colored map. 4 pl. 18 fig. Vol. 6 of *Beiträge zur geobotanischen Landesaufnahme der Schweiz; herausgegeben von der Pflanzengeographischen Kommission der Schweizerischen Naturforschenden Gesellschaft. Zürich.* (Verlag Hans Huber, Bern.)

**Eduard Rübel.** 1930. Pflanzengesellschaften der Erde. 464 pp., 242 fig. Colored map of the climatic formation classes of the world. (Verlag Hans Huber, Bern.)

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a third or a fourth.   A generally practicable classification cannot be based on one or on a few factors.

Moreover, the single factor acts differently when accompanied by other factors.   Absolute figures tell very little about a factor as its effect is so variable; it is relative in its action and varies in relation to other factors.   Its relative importance is influenced by other factors; for example, an annual precipitation of 50 cm. is hydromorphal in Ireland, xeromorphal in Colorado. Here temperature strongly influences the effect of the moisture factor.   The combined effect of factors often results quite otherwise than the individual factors seem to indicate.

Thus it is always necessary to investigate whether the factor under consideration may not be modified or replaced by others, completely or in part.

This replaceability is of great importance.   It permits a certain plant community to continue to thrive in places where several of the factors have changed; it renders possible the spreading of communities; it facilitates the migration of species.   It proves itself to be an impediment in the characterization of vegetation, because we instinctively use single factors, emphasizing one more than the other.   Thus a place is differently classified according to whether the changed or the unchanged factors are emphasized.   It may therefore appear that the same plant community is found in two quite different habitats.   In reality the habitats are the same, or rather the resultant is the same in the two localities, but arrived at by different factor-complexes or factor-summations: thus $2 + 2 + 2 + 2$ and $3 + 5$ both give the sum 8.

A further complication is encountered in the fact that the plant is not passive towards these influences, but reacts actively.   Another complication lies in the fact that some plants are stenecious and require very exactly adjusted habitat conditions, while other plants are euryecious and are not particular about the habitat.

Replaceability is theoretically accepted by everybody as a matter of course, but practically the possibilities of replaceability and the resulting consequences are always apt to be forgotten; hence they need constant and repeated emphasis.   In the classification of vegetation on a climatic basis little consideration is usually given to the fact that edaphic factors decidedly change the effects and alter the results of climatic factors.   In order to avoid errors in this respect Schimper set apart from his excellent climatic classification (Gliederung) certain plant communities as edaphically conditioned and as unfitted for climatic classification.   But the difficulties dissolve when the replaceability of factors is duly considered.   The communities put aside will then fit in well, as may be seen in my works just cited.

It must also be borne in mind that single factors do not act simply but have multiple action.   Wind, for instance, not only acts mechanically on plants, but also carries off moisture.   Many similar cases may be cited.   Every sort of replaceability occurs; climatic factors are replaced by edaphic or biotic; edaphic factors by climatic or edaphic, and so on.   Within each

groups of factors the individual factors may complement and replace one an-
other.

Precipitation may be replaced by humidity or fog. Deserts in the vicinity
of sea coasts which receive almost no water in the form of precipitation often
support a vegetation made possible by fog. On the rainless coasts of northern
Chili and Peru thick wetting fogs prevail during the winter and make pos-
sible grassland vegetation. Similarly there are the redwood (*Sequoia semper-
virens*) forests of California made possible by the Pacific fogs. In districts
in Switzerland, deficient in precipitation, forests of the beech (*Fagus sil-
vatica*) occur within mist belts, as for instance, around the knee of the Rhone
(described by Gams) and elsewhere. Nor is mist necessary for such results;
high atmospheric humidity, which has not condensed into droplets, acts in the
same way. Large portions of Great Britain have little precipitation shown
by absolute figures, but the air moisture in this oceanic country replaces pre-
cipitation by reducing the transpiration of plants. Low temperature acts in
much the same way; with 60–100 cm. annual precipitation forests thrive in
Great Britain which would require 110–150 cm. or more under conditions
existing in eastern North America. Transeau's precipitation-evaporation
coefficient is above 100 in both cases.

Wind has a drying effect like that of reduced humidity and hence the
former may replace the latter. In spite of high precipitation summations and
high atmospheric humidity, vegetation may wilt, that is, show a moisture de-
ficiency, if strong air movement prevails.

Among edaphic factors a physically light soil may be replaced by clay soil
containing lime. The chemical element calcium seems to compensate for the
physical lightness of the soil. This depends upon changes in the state of dis-
persion of the solids in the soil. The two-valenced calcium ion brings about
coagulation in the solid dispersion of a heavy clay soil and thus effects a
change to a coarser state.

Besides this, lime acts in other ways: it neutralizes sour soil; it stimulates
the activity of microorganisms; it frees nutrients by basic exchanges. The
main activity of the calcium ion, however, seems to consist in making the
whole soil system one of coarser dispersity, thus replacing a light soil in its
action upon the plant. A similar example is the replacement of physical
drought by "physiological drought." Both result in the reduction of root
activity.

An interesting example of the action of a biotic factor where plants re-
place man in making fallow fields is found in Colorado, where Shantz and
Piemeisel report the action of the well known fairy ring fungus. The fungus
kills the primary vegetation instead of man doing it, and produces thus the
fallowness of the soil. On these fungal fallow fields a succession takes place
quite similar to that on abandoned ploughed land. Weeds are followed by
a stage of perennial herbs and finally the short-grass turf is reestablished.

These examples taken within a group of factors may be followed by others

showing replacement between different groups, especially the very important interchange between climatic and edaphic factors. Dry lime hills in central Europe show on their south slopes a vegetation characteristic for southern and more continental countries. This is due to the dryness and warmth of the lime soil which replace the southern Mediterranean climate and thus a southern climate is reproduced edaphically by dry warm soil. Inversely, coolness and moisture in the soil of a hot southern climate produce northern vegetation. Throughout the Mediterranean region and far into the African desert the vegetation along the water courses keeps the character of a northern mid-European deciduous forest, as seen in the deciduous poplar stands in the Libyan oasis of Siwa or in the Algerian torrent beds of Beni Ounif. These deciduous forests in the deserts belong ecologically to the deciduous summer forest type (Aestisilvae). Although regionally situated in a generally desert climate, the cool moist soil factor connects these communities with the vegetation of the more generally northern climate. The high specific heat of water gives it a strong compensating effect and thus water plants are able to be cosmopolitan, largely independent of the climate. Edaphic water replaces several climatic factors. In hot regions water acts as a refrigerant, replacing lower temperatures; in cool regions water stores its summer heat and replaces higher air temperatures during the cool season.

Sandy soil has a similar compensating effect, in humid regions acting as a factor for dryness. Asparagus cultures, which perish in ordinary soil in the humid Swiss climate, thrive in sandy soil. In dry regions sands mean a moist habitat. In the dry short-grass plains sand permits the development of wire grass and bunch grass associations (Aristidetum longisetae and Andropogonetum scoparii) communities that require more moisture.

The compensating effect of water is seen not only in connection with the temperature factor, but it also extends to a certain degree to the whole complex of " oceanic climate."

Reed swamp communities (Phragmiteta) find such optimal conditions in oceanic Ireland that they invade even potato fields. This climate is so well replaced by deeper and deeper water that they thrive all over Europe, extending to the continental east in the Roumanian Danube swamps and growing in large quantities in the Caspian Sea. Climatic " oceanity " is also replaced by depth of soil. Deep soil does not dry out rapidly; temperature changes do not penetrate it easily; its water content does not vary quickly. In contrast, shallow soil behaves like continental climate. In the climate of Zürich forests of the beech, *Fagus silvatica*, find optimum conditions and they develop on any soil, while in England they show a preference for chalk soil. The lack in beech climate is there replaced by the dryness afforded by the lime content of the soil. Many a plant is indifferent to soil in its optimum climate but becomes an indicator of this or that factor where parts of its needed climate are lacking and are replaced by this or that edaphic or biotic factor; the habitat complex is the same but is differently made up.

A powerful biotic factor replacing climatic ones is man. Tropical and subtropical climates are often replaced anthropogenously by heating hot-houses, by constructing irrigation works. Cool moist climate produces ever-green meadows above the timber line, and beyond the poleward limit of trees, and the effect of this climate can be replaced by the scythe and by cattle tooth, which are equally as hostile to forest growth as is alpine climate. Thus low-land meadows may not be segregated from alpine meadows. Many communi-ties which occur under a favorable climate as independent associations, such as heath vegetation, under a less favorable climate are found only beneath the shelter of trees as an undergrowth of forests.

Biotically the natural edaphic nutrients can be replaced by manure which also to some extent replaces the effect of water. A heavily manured meadow produces a vegetation that closely resembles a very humid grassland. Many salt plants will grow in saltless soil, and calcicolous plants in limeless soil if man prevents competition from better adapted species. The silicicolous alpen-rose (*Rhododendron ferrugineum*) thrives very well on calcareous soil when competition is removed; and the same is true in the case of hochmoor plants.

All these replaceabilities which we have considered have a decided effect on the law of the minimum. If one factor intensifies the action of another, the minimum of the latter is less than it would be without the help of the former. The contrary effect is possible when the accompanying factor results in raising the minimum. A species or an association may be adapted to a climate and may thrive in a soil when not limited in space, but it may lack strength to compete with new invaders. To be successful it must not only possess ability to thrive but also in addition the power to combat competitors. Only if the environment is sufficiently favorable to give strength enough to enable the plant to resist competition is the minimum necessary for success attained. For instance, in New Zealand the old established natural vegeta-tion has been expelled by invaders that have come in with the white man. These invaders have increased by their competition the necessary minimum above the favorable environment formerly present. This has caused a change, a dispossession.

On the Great Plains an annual precipitation of 40 cm. is enough to make possible the grama grass association (Boutelouetum oligostachyae), but is under the minimum water supply necessary (50–60.cm.) for the bunch grass association (Andropogetum scoparii). When another factor, sandy soil, comes in, as has been noted before, it changes the water minimum so that the 40 cm. of precipitation suffices for the bunch grass.

A similar case is seen in the human communities of North American In-dians which prospered very well in their habitat until the white man came. Then they had not the strength for competition with the European races, and this competition so raised the minimum necessary for existence that they have almost disappeared.

The law of the minimum and the replaceability of factors are valid not

only for plants and plant communities; they apply likewise to mankind. Each of us must endure, shape, and live his own factors' minima and their replaceability. Brain is a master factor in man, but to a considerable extent it may be replaced by money or by credit or by connections or even by bluffing, especially in politics. Conceit and bumptiousness often replace real knowledge. With good replacements minima can be bettered and life improved. In becoming older we replace the elasticity of youth by the growing experience of age. A little bit of talent for organization may replace many missing factors. Good humour is a splendid replacer of many factors we do not have or which we lose in the current of years. One may study one's own characteristic qualities, their minima and replacements. This is self-knowledge. If one traces the working of these factors in ones ancestors or in other families it is genealogy. But if a similar investigation be centered upon plants and plant communities it becomes a most interesting chapter in plant ecology.

# EXPERIMENTAL ECOLOGY IN THE PUBLIC SERVICE

FREDERIC E. CLEMENTS

## INTRODUCTION

During the past quarter of a century dynamic ecology has come into wider opportunities of service in such well-established fields as forestry, agronomy and grazing and has contributed steadily to the foundation of those more recently developed, such as erosion control and water supplies. With the present great expansion of federal projects has gone a corresponding increase in the utilization of ecological methods and concepts, even when this term has not been employed. How widely the comprehension of the basic role of ecology in human affairs has spread may be seen from the statements of progressive thinkers in various fields. Professor Murchison takes both plant and animal ecology into account in his "Handbook of Social Psychology," Mr. Wells has said that "economics is a branch of ecology," and General Smuts stresses its significance in "Holism and Evolution." Elsewhere he has stated that "Ecology must have its way; ecological methods and outlook must find a place in human government as much as in the study of man, other animals, and plants. Ecology is for mankind."

The essence of ecology was long ago said to be measurement, experiment, development (dynamics) and synthesis (Clements, '05). It is obvious that much that bears the name of ecology possesses these qualities not at all or in small degree, as is also the fact that they may be present without the name. From its very synthetic nature, ecology is not to be regarded as a specialized field comparable to physiology or morphology or even zoology, botany or geology, but as a point of view and a plan of attack. As such, it justifies fully the statements quoted above and embraces all problems in which life and its environment are concerned. It is not only inclusive in comprising all the aspects of the cause-and-effect sequence in individual and community, but likewise in embracing all organisms from protophyte and protozoan to flowering plant and man. In this conception, no other term possesses the intrinsic significance of ecology, as none other denotes the unremitting search for causes.

## CONCEPTS

These have been discussed in detail elsewhere (Clements, '16, '20; Weaver and Clements, '29; Clements and Shelford, '35; Phillips, '34, '35), and hence only the more salient principles require emphasis here. The first of these is that the community is a complex organism of a wholly different order from the individual plant or animal, but nevertheless an organic entity with functions and structure. As a whole, it is not merely greater than the

sum of its constituent species and individuals, but these in turn are something different in the community from what they are detached from it. The universal or final control of all community life resides in the climate, in conformity with which the grand communities are termed climaxes, while the immediate control may lie in land-form, soil, or some activity of that super-dominant, man. As a consequence of its response to these in varying degree, the climax exhibits a complex structure determined by its development, which in turn is an outcome of the functions of the community. These interact to constitute the growth and behavior pattern of communities of all degrees and of all kinds from the simplest family of unicellular organisms to the highly specialized societies of man. The mere enumeration of such functions suffices to show that they are universal in character and that most of them possess at least a general human connotation. The complete list comprises aggregation, migration, reaction, coaction, competition, cooperation, disoperation, ecesis, invasion, and succession, the last being an integration of all others and representing in the community the role taken by growth and development in the individual.

## REACTION

The driving forces in development or succession are to be found in coaction and reaction, the first comprising all the effects of the associated organisms upon each other and the second their modifying influence upon the factors of the habitat. All favorable coactions involve cooperation in some degree, while unfavorable ones give rise to disoperation of varying kinds, among which competition is of the first importance. In the reaction that marks each life-form stage or associes of a sere, cooperation is paramount at first and the resulting reaction consolidates the position of the community concerned. Continuing reaction leads to disoperation and competition with the consequence that the next stage enters and gradually takes possession, this alternation of effects persisting until the climax is reached, when cooperation with secondary competition maintains the characteristic stability. The initial investigation of plant competition has disclosed the details of the process for a number of life-forms, but a similar comprehensive and intimate study of reaction is yet to be made. While this field was long ago organized ("Research Methods in Ecology," 1905; "Plant Succession," 1916), adequate quantitative studies are still few in number and these deal with a single factor as a rule instead of with the ecial complex. It is obvious that reaction is universally the critical function wherever the relations of community and soil are concerned, but this is nowhere so important as when the soil itself is to be conserved, as in the manifold types of erosion.

## COACTIONS

These embrace three different categories with respect to the organisms concerned, namely, interactions between plants, those between plants and

animals, and those that concern animals directly or primarily.   The last
do not require consideration here, while the first have already been mentioned
as involving chiefly cooperation and disoperation, competition being the
chief form that the latter takes, though parasitism plays a subordinate part.
The most significant coactions between plants and animals are those in
which the latter take the active role as consumers of plants for food, often
producing striking community effects.   However, these are relatively
insignificant in nature and rarely become considerable or controlling until
man enters the situation by virtue of the various kinds of disturbances that
he exerts.

   As with the other animals, the coactions due to man are almost wholly a
matter of destruction, direct or indirect, but he has a wider range of processes
at his command and applies them on a much larger scale.   Primitive man
had at his disposal but the single tool, fire; the nomad added grazing, and
the lake-dweller, clearing and cultivation.   Construction for irrigation could
hardly have antedated the historic period and the development of roads on a
large engineering scale came very much later, as did draining and impound-
ing in any considerable degree.   In spite of the great variety of concrete
coactions, all human types of disturbance may be summed up in those
mentioned, and these are merely different ways of intentional or uninten-
tional destruction.   In short, man may be said to destroy to plant and to
plant to destroy, the chief exception being found in his growing tendency to
check destruction by erosion control.

## SUCCESSION

   Under primitive conditions, the great climaxes of the globe must have
remained essentially intact, since fires from natural causes must have been
both relatively infrequent and localized.   Succession was far less general
and was represented chiefly by priseres, especially in water and dune sand;
subseres were few in number and small in extent.   They became universal
features only as man extended his dominion over nature through disturbance
and destruction, and they are permanent today in the degree to which these
forces are continuous or recurrent.   From the very nature of climax and
succession, development is immediately resumed when the disturbing cause
ceases, and in this fact lies the basic principle of all restoration or rehabilita-
tion.   Left undisturbed, every bare, denuded or seral area begins its slow
but inevitable movement to the climax wherever the latter has not been
destroyed over too large a territory to permit the mobilization of the
successive populations.

   As a consequence, it is only necessary for the ecologist to know the course
and rate of each sere in order to control it or at least shape it to the desired
purpose.   The natural process once thoroughly understood, it becomes
possible to retard or accelerate it, to "telescope" or hold it more or less
definitely in one stage or to deflect it in any one of several possible directions,

or finally to destroy it and allow the process to start again within the limitations set by the species available.    Moreover, it may be manipulated as a sequence of natural communities, it may be modified by the insertion of introduced or cultivated species, or once so modified, it may again be restored to its proper development in the climax.    As the final stage of a sere, the climax is less flexible in terms of manipulation, but it is capable of similar control; it can be protected and held against all but climatic change, as in research and wilderness areas.    It can be enriched or impoverished, and it can be destroyed in such a way as to reproduce itself or so completely as to render this impossible, thus permitting a wide range of substitutions within the limits of climate and soil.    In short, as an instrument for the control of the entire range of human uses of vegetation and the land, succession is wholly unrivalled.

## EXPERIMENTAL SUCCESSION

It is well understood that the body of knowledge concerning succession and climax has been built up chiefly by the method of comparative observation, though much of this ·has been directed to the quasi-experiments so abundant in nature, as well as to those unintentionally set up by man.    A direct experimental attack upòn succession by any one individual has been discouraged by the length of time embodied in a single prisere, to say nothing of the expense and territory involved.    Even the much shorter span of most subseres has been too long for the individual investigator as a rule, and no adequately quantitative and complete study has yet been made, though some may approximate this goal (Clements, '10).    Probably the most comprehensive installation for such experimentation has been the cooperative grazing project on the Santa Rita Range Reserve in Arizona, which has been carried on since 1918 by the Forest Service, Biological Survey, University of Arizona and the Carnegie Institution.    However, this is necessarily confined to the changes due to short climatic cycles, to grazing and to rodent coactions, and the subseres from initial denuded areas are relatively few and minute.

From the above, it is evident that great national projects that promise a lengthy or indefinite period for their realization constitute an opportunity for experimental succession that may never come again.    Consequently, dynamic ecologists are justified in feeling that the time and energy spent on such problems will bring a double return.    The immediate and larger reward must spring from the service that ecological concepts and methods alone can render, but along with this is the chance to carry out experiments in vegetation on a scale and for a period never before possible.    These are in essence basic social-economic studies that deal not merely with the setting, behavior and welfare of human communities, but also exemplify the great ecological processes that constitute society and foreshadow the control that man must achieve of such opposed community functions as cooperation and disopera-

tion.   Hence, it is peculiarly fitting that the present issue should honor the
man who was the pioneer in applying the successional concept to American
vegetation (Cowles, '99, '01, '10).

## METHODS

These chiefly concern the community, though standard phytometers
regularly consist of individual plants and indicator values rest upon the
response and reaction of the species-individual or specient.   The immediate
objectives are the dynamics of plant and community as expressed in func-
tions and processes, which are summed up in development as integration or
growth and structure as the final outcome.   Development in turn comprises
the life history or ontogeny of specient and climax, and their evolution or
phylogeny.   As to procedure, investigation necessarily advances by analysis,
with the realization that this is important in the understanding of the simple
or complex organism only in so far as it contributes to synthesis.   Indeed,
there can not be too much emphasis upon the statement that ecology has the
synthesis of cause-and-effect relations of organisms as its one great goal.
This is obviously as true of the habitat as it is of species or community and
it applies with all the more force to the biotic community or biome, with man
as the super-dominant.

While complete objectivity is the supreme goal of all science, it is even
more essential to ecology in view of its inclusive nature.   It can be secured
only by the rigorous methods of physics and chemistry, but the obstacles in
the way of applying these to life and its setting may sometimes appear
insuperable.   Thus, in the case of such a basic factor as light, physical
methods still leave much to be desired, while the accurate determination of
response by the whole organism to it is at present impossible, at least outside
of an aqueous system.   In spite of this, measurement and experiment by
means of constantly improving methods and instruments constitute the
distinguishing mark of dynamic ecology and afford the sole procedure by
which it may gradually achieve much of the objectivity of physics and
chemistry.   As with these, interpretation and hypothesis must always play
a legitimate role, but primarily for the sake of guiding further experimenta-
tion, which in all instances must be considered the final arbiter.

Measurement in the broadest sense of the word is indispensable through
the whole field, whether it involves the physical factors of the ece as causes
or the responses of plant or community under existing conditions or subject
to varying degrees of control.   It is even more intrinsic to experiment,
which becomes objective in nature only as it is quantitative in method.
The immediate purpose of experiment is analysis of complexes, in terms of
functions and processes, for which it is imperative to take into account
natural conditions so-called, partial control of one or more factors and func-
tions in field and garden, and complete control within the limits of laboratory
technique.   As has been emphasized elsewhere, the out-of-doors lends itself

with difficulty to control experiments, while the laboratory is unsatisfactory in not permitting the use of complete organisms in the normal factor complex.  In consequence, both must be utilized in the proper degree of coordination and preferably by the same group of experimenters, which often demands cooperation.  As to the community, laboratory control is out of question for the most part, but close approximations may be attained in greenhouse and garden in the form of miniature replicas.

## PHYTOMETERS AND INSTRUMENTS

It has become increasingly evident that the analysis of habitats by means of physical instruments alone is far from complete, partly because of the inadequacy of most instruments but chiefly because of the necessity for expressing physical and chemical measures in terms of plant functions. This is possible only by means of the varied control afforded by phytometers (Clements and Goldsmith, '24), which must be assigned prior rights in all such studies, while instruments, though indispensable, must be relegated to a secondary position.  Quite apart from their unique value in rendering the judgment of organism or community upon factor or complex, they also disclose the nature and degree of response and give a significance to physical units that can not be otherwise secured.  For single factors community phytometers are often desirable and these may range from sod cores and sown and planted quadrats to closures of several sorts.

## QUADRATS AND CLOSURES

In the thirty years since the proposal of a comprehensive system ("Research Methods," 1905), quadrats and transects in a variety of forms have become the customary procedure in all quantitative studies of vegetation. They have been extended and modified for special purposes, and the methods of charting improved in accuracy and speed, first by means of the pantograph and then by using the overhead camera.  The latter is definitely indicated in all communities where stature and layering are not too great, or even in some of the latter when combined with the bisect.  List or census quadrats have little or no value in dynamic ecology by comparison with the permanent type, which are conveniently grouped as cut or clip, denuded, and process quadrats.  The first are designed to measure yield, the second to trace succession, and the third to follow and evaluate disturbance processes in particular.  By contrast with surface relations, those of depth are determined by means of the bisect or better still by the bisect-quadrat.

The usual type of closure is the exclosure, a fenced area of suitable size which provides protection against the coactions of one or more groups or species of animal.  The enclosure is similar in design, but is used to restrict animals to a definite area to permit the direct study of their influence, while the isolation transect is a combination of small units opened and closed respectively each year ("Plant Indicators," '20).  As a rule, exclosures are

a few acres in extent and consist of two units, one fenced to exclude cattle and the other, the larger rodents as well. Because of the protection afforded, they serve also for the installation of process series, which permit analyzing the effect of the various processes in disturbance and recovery.

Changes over an area larger than those recorded by quadrats and transects of various sizes are mapped directly or by means of photographs. The first employs plane-table and alidade, but its advantage in permitting the insertion of greater detail is often more than offset by the time and labor involved. Photographic mapping is incomparably much more rapid and can be made to supplement the quadrat views with the desired adequacy. For maximum detail, an elevated platform is utilized, preferably on an auto-body for mobility, though a step-ladder may serve as well. To permit tracing the changes from season to season or year to year, the exact location of the tripod is fixed, originally by means of three stakes as in a tristat, and later by a single one at the end of a plumb-line, or by a focusing stake and centering dot on the ground-glass. Panoramic cameras may be employed in this work, though a certain allowance must be made for marginal distortion, but panoraming with a Ciné-Kodak is much more satisfactory, especially when Kodachrome film is used, since both the large scale and color aid greatly in revealing details. Finally, community maps on a small scale are best made from an airplane, but these naturally must be combined with detail maps and other records made on the ground.

## INDICATOR METHODS

The role of comparative observation in the analysis and correlation of vegetation is a large one when it employs plants as indicators of conditions and processes and hence of land use and recovery. Every species is an index to the physical factors of its habitat, whether climax or seral, to the effect of disturbance, the course of succession, and often also to the influence of animal coactions. As such, its value is greater in terms of the community to which it belongs, and hence the latter constitutes the best type of indicator, since it integrates the response of a considerable number of species as dominants. The kinds of indicators and their significance have been discussed in "Plant Indicators" at some length and consequently it is desirable merely to emphasize their role in connection with the utilization and conversion of the land.

The indicators of paramount importance are the dominant species that constitute a climax, since they bear the unmistakable impress of the climate in the corresponding life-form, viz. tree, shrub, and grass. The same correlation extends into subforms, such as coniferous, deciduous, and semper-virent trees and shrubs, and sod or bunch forming grasses. As a corollary of the first significance, climax indicators express the type and degree of climatic control and the problems that confront man in his utilization of the region concerned, either in maintaining the climax or in modifying or replac-

ing it permanently. The indicators of the various stages of succession toward the climax are often of equal importance, inasmuch as they reveal the course of development and provide the readiest tool by which the return of the climax may be hastened, retarded, or prevented, or the movement deflected into another path. Of seral indicators the most practicable are the dominants of subseres, since these arise from disturbance. They not merely denote the nature of the disturbing process, but likewise its course and the manner of manipulation necessary to bring about the desired type of permanent community, which is often the subclimax, or more rarely a seral stage.

As examples of the above, there are a number of subclimax trees of greater commercial value than the climax dominants that they have replaced, notably longleaf pine (*Pinus palustris*) and Douglas fir (*Pseudotsuga taxifolia*). Such stands can be maintained against the return of the climax dominants only by means of fire, but when this tool is employed too frequently, unintentionally or otherwise, the subclimax is itself displaced by an earlier seral stage. The same general relation prevails on grazing ranges, in which short-grasses have everywhere increased under intensive utilization, but are in turn dispossessed by less valuable seral dominants under serious overgrazing. The mid-grasses relict in such disclimaxes not only indicate the original mixed prairie climax, but their condition and abundance also determine the treatment needed to restore them to their proper rank in the regenerated range.

## Fields of Application

### GENERAL RELATIONS

While ecological methods and concepts have been utilized for some time in agriculture, forestry, and grazing, their use has been much extended during the past two decades, largely in consequence of the growing appreciation of quantitative values, as well as of the need for cooperation between dynamic ecology and the specialized fields. The latter in particular has led to the recognition of the role played by different types of communities in terms of influences or reactions, with the logical though not altogether desirable result that erosion projects have been initiated in all three fields. Grazing had already come to play an important part in the administration of national forests and was necessarily concerned in the plan for the so-called desert homesteads. It is likewise the major consideration in the organization of grazing regions and districts on the public domain.

Land classification for optimum use has been conspicuously absent in the past, but critical conditions in the West at present must bring some intelligent consideration of its necessity. This is indispensable to the selection of the regions and the actual areas to be protected by the wind-breaks of the so-called shelter-belt, and it is equally involved in all projects for erosion control and water conservation. Less dramatic but still of

great importance is the protection of modern highways against erosion and the consequent economy of maintenance, and with this must go a proper concern for ornamentation. In addition to highways, control and beautification through landscaping are needed in practically all natural parks, whether national, state or county, and control and restoration are requisites in many other units, such as recreation grounds, game refuges, research and wilderness areas, etc. Finally, as the present crisis demonstrates, climatic factors often play a decisive part in all uses of the plant cover and no project is complete without taking definitely into account the wet and dry phases of the 11-year cycle in particular.

It is patent that the above fields and related projects are largely a matter of specialization and to a certain extent of tradition in terms of administration. Any one of the major projects may and usually does broaden its scope to include areas that belong in the strict sense to the others and any natural limits disappear. While this has been inevitable up to the present, it is regretable and must be remedied to an increasing degree if the best practical and scientific results are to be obtained. It is quite impossible to deal adequately with one type of vegetation in any region without consideration of the others, while in terms of the basic processes involved, all climaxes are closely similar. This is well exemplified in the case of the shelter-belt, in which the task devolves upon the forester by virtue of the use of trees, though the climax and climate concerned are those of grassland. Hence, while the following treatment is organized on the basis of projects, it can not be too strongly emphasized that this violates every canon of dynamic ecology and that a proper ecological synthesis is imperative if rehabilitation and restoration are to achieve the necessary measure of success.

## LAND CLASSIFICATION AND USE

The major features of a comprehensive land policy based upon the methods of dynamic ecology were long ago outlined (Clements, '10, '20) and only the essentials need to be repeated here. The first of these is that land must be classified on the basis of optimum permanent use, and the second that the lands of a general climatic region or district are to be correlated in such a manner as to supplement each other. The third principle is that proper heed must be paid to the climatic cycle in classifying and much greater weight assigned to the unfavorable dry phase ("Plant Indicators," p. 266, 344), which demands a complete reversal of the existing practice. The fourth essential is that land should improve or at least not deteriorate under utilization, and the last is that it must maintain an assured basic role in the economic-social welfare of the region.

It can not be too strongly emphasized that no classification worthy of the term has ever been applied to the lands of the West in particular. Even the one or two endeavors have been rendered abortive by political pressure,

the demand for haste, and the general lack of a trained personnel. However, the classification under the desert homestead act did recognize the unique importance of native vegetation as the basis for evaluating land, and hence marks the first real step in advance. The natural plant communities are not merely the best integrators of the effects of climate and soil, but axiomatically they are also by far the best judges of these two complexes in terms of plant production. When reinforced by the composite judgment of all the practical experiments in a region and checked by an understanding of the inevitable climatic cycles, they can be trusted to furnish the basis for the highest type of social-economic development possible in a particular climatic region.

No such convincing proof of the unwisdom of attempting to settle land by the trial-and-error method has ever been afforded as that now available throughout the Great Plains, but disasters comparable in most respects have attended every great drought period, as in the early seventies, the ,nineties, and 1917–18. Drought itself is inevitable at more or less definite intervals (Clements, '16, '21), but the major damage is done by man's failure to heed the climatic indicators as to use and to control the destructive processes that he sets up, and his incurable optimism as to the effect of cultivation upon rainfall (Clements, '23; Kollmorgen, '35). Some of the damage wrought by the failure to classify land and direct its use may still be undone by applying the proper principles and methods, not merely to the new apportionment of the public domain but even more helpfully to the reclassification of all so-called marginal lands and their rehabilitation on the basis of the climax vegetation.

### GRAZING AND THE PUBLIC DOMAIN

The first application of quantitative methods to the problems of grazing came in 1905 with the organization of the national forests and the necessity of finding a basis for grazing allotments, which led to the use of quadrats in connection with reconnoissance and especially on the grazing reserves that were soon established. The latter were designed primarily to insure regulated utilization together with the gradual improvement of the range, and it was not until 1918 that an ecological system of closures, quadrats and transects was installed on the Santa Rita Reserve in southern Arizona, as well as in the northern part of the state, at the Mandan Station in the Great Plains, and elsewhere.

Because of their low stature, relatively short life-span, and quick response to conditions, grasses lend themselves more readily to experimental studies than do the taller and slow-growing trees, though the principles and methods are necessarily the same for both. While the major purpose in the study of grazing ranges is to secure the proper balance between use and improvement, this can be obtained only through certain intermediate objectives. The chief of these are a working knowledge of grazing types in terms of climax

and climate and of the effect of succession, an understanding of the seasonal and competitive relations of the dominant grasses and associated forbs, the coactions of cattle with especial reference to overgrazing, the effect of rodents and their predators, the role of drought, the moot question of direct improvement by sowing and planting, particularly of foreign species, and the reaction of the grass cover itself upon runoff, flooding, erosion, and water supplies. In short, a grassland climax embodies all the responses and effects of a forest, though in different form and degree.

Even the most succinct account of the progress of research in these respects is impossible here and it must suffice to sketch in the boldest outline the chief methods and results. First of these is the exclosure, which in combination with the enclosure, or pasture in the regular form, permits a relatively accurate measure of the effects of the several processes involved. The simplest exclosure affords protection against cattle alone and makes possible the measurement of the consequent improvement or recovery, its rate, the effect of the grazing practiced, the outcome of competition between the preferred grasses and the less palatable forbs, etc. The part taken by rodents in all this is often very considerable and consequently rodent-proof or total-protection exclosures are added to the installation. Impressed upon all these effects, obscuring or emphasizing them, are those of the year, which in turn vary greatly with the phase of the climatic cycle and require measurement likewise, such as is provided by the isolation transect or cycle exclosure ("Plant Indicators," 1920). However, all of these deal more directly with effects than with causes and for an adequate ecological analysis of the processes involved in overgrazing as well as restoration, it is necessary to isolate each and follow its course under control. This is accomplished by means of a process or conversion series, which may be installed in any exclosure, but is most conveniently duplicated on each side of the boundary fence between cattle-proof and rodent-proof units. Such a series may deal with one or more of the processes of major importance in the type concerned, but preferably it should take them all into account for the sake of a complete and objective analysis. The most important·of these are grazing, usually simulated by clipping, burning, erosion, denuding, such coactions as trampling and burrowing, competition, seeding and planting.

Employment of ecological methods of measurement and experiment during the past two decades has disclosed a number of principles that appear to be of universal significance, some of which may well be regarded as axioms. Chief of these is the irresistible impulse toward the climax, which can be slowed or halted only by deep-seated disturbance or by unfavorable climatic swing. A major corollary is that the climatic life-form everywhere maintains its ascendency in the absence of disturbing processes or reasserts it as soon as these are removed. So far in many hundreds of cases no exception has been found to the rule that grass dominants vanquish forbs and annual grasses on the one hand, and bushes or shrubs on the other whenever

grazing, fire or similar destructive disturbances are prevented (Clements, '20; Clements, Weaver and Hanson, '28). The correlation of control with climate is even more exact, operating within the grass life-form to the extent that mid-grasses, such as *Stipa*, *Sporobolus* and *Koeleria*, yield to short-grasses in semiarid climates and to tall-grasses in more humid ones under the impact of grazing, mowing and fire, and reclaim their climatic dominance when these forces are eliminated. Another expression of this principle is found in the fact that the grasses of a particular climax are the best adapted to its climate and have a distinct advantage in terms of competition over introduced ones. This applies with especial force to the world-wide search for grasses to regenerate the open range and to aid in erosion control. The chances are all but decisive against the success of such efforts at introduction, as the actual attempts in the past have demonstrated. Crested wheatgrass (*Agropyrum cristatum*) has often been cited as a warrant for such a procedure, but all the evidence available indicates that it can persist in the face of the competition of the indigenous grasses only when man aids it by cultivation or otherwise.

### PUBLIC DOMAIN

At the present moment the unreserved public domain consists almost wholly of semiarid or arid grassland and desert, valuable only for grazing and as watershed, or not inconsiderable portions for neither. The value of practically all the usable portions has been diminished by overgrazing and erosion, aided by recurrent drought, and the task of the new Division of Grazing Control is to develop systems of range management that will restore and conserve the natural forage crop. For this, a comprehensive system of exclosures has been proposed, designed to evaluate the present carrying capacity of the various grazing types, the rate of recovery to be expected under proper regulation, and the methods of securing the best balance between utilization and conservation. A necessary adjunct is the use of indicators to record existing conditions and their gradual change into grazing communities of the desired composition and yield.

The several grazing regions correspond to major differences in the structure of the prairie formation, while the forty odd districts represent more localized variations in the grass cover. While improvement in the forage yield and carrying capacity of all of these will follow the principles already indicated, the actual situation in any district must be measured as accurately as possible to prevent continued overstocking and consequent postponement of the regeneration sought. The immediate need may be met by means of production exclosures to disclose the present yield under protection, as a basis for preliminary regulations designed to bring about recovery as rapidly as possible. These may be readily converted into protection exclosures that permit ascertaining the role of rodents, and to these may be added the conversion series designed to demonstrate the part played by the processes of disturbance and of recovery, both natural and

artificial. Finally, cycle exclosures in the form of isolation transects are essential to determining the cycle of production, which affects economic conditions in the stock industry more than any other single factor.

## SHELTER-BELTS AND WIND-BREAKS

The controversy that still rages over the wisdom of the shelter-belt project may well be regarded as a major argument in favor of making the experiment. The need for relief from want as well as from dust storms requires no argument and the other moot questions are susceptible of objective demonstration in the course of providing the succor demanded by the conditions. It is evident to those with wide ecological experience that the merits of the project are overestimated by those who feel that tree planting is a panacea, just as its difficulties and impossibilities are alone visible to the critics of the experiment. Granted that the form in which the plan was first made public was impossible, the fact remains that trees have been grown with much success within the limits of the belt proposed and that such wind-breaks have been of value in a number of the respects claimed. No qualified student of vegetation, in its water relations especially, expects wind-breaks to modify the general climate and particularly in the direction of increased rainfall, but the local influences have already been demonstrated and some of them measured (Bates, '11).

The ecologist familiar with the region recognizes that nature still maintains trees in portions of it, notably in valleys, in the higher foothills to the west, and in areas to the east or north where rainfall is greater or evaporation and transpiration less. Planting has had notable success in the sandhills of Nebraska, offset in some measure by corresponding failure in other sandy stretches, and the earlier establishment of wind-breaks has a considerable number of successes to its credit in spite of the drawbacks of a cooperative arrangement (Wilson and Cobb, '23). Trees can be grown in the zone as now outlined, though forests cannot, and the major questions are those of extent and size. These can be answered only by the actual trial, in which the selection of proper sites and suitable species are the paramount problems. A close second in importance is the preparation of the ground, the form and structure of the belt, protection against animals, and the precautions against the return of the climax grasses. Finally, the unique value of the project as an experiment on a grand scale will be lost if every consideration is not given to obtaining the most comprehensive and objective measures of effects, in so far as these have to do with reactions upon air and soil, the competition between wind-breaks and crops, and the coactions of animals.

From the very nature of the grassland climate and climax, it is probable that extensive areas within the belt will be inhospitable to trees and that with these recourse must be had to the restoration of the original grass cover or an approximation to it. This is even more certainly the future of marginal farm lands to the westward, which are destined to return to grass by

default, or better by means of a comprehensive and properly articulated plan for rehabilitation. The entire region between assured agriculture on the east and the mountains has been the center of a cyclic ebb and flow of human populations to the point where illusion as to its possibilities of utilization for cereal crops is no longer possible. However, this tragic process is bound to continue until the clear evidence of climate and climax is heeded, the land classified as grazing country and its organization into proper holdings directed by the federal authority.

In the three great aspects of the shelter-belt project, ecological considerations necessarily reign supreme. The method of indicator communities is indispensable to the selection of site and species, and it may be epitomized in the statement that climax areas are the most difficult of conversion and control, while seral, subclimax and postclimax sites hold out the greatest promise. The preparation, development and maintenance of the wind-break communities are almost wholly dependent upon the understanding and control of such processes as reaction and coaction, in which man may easily become the adverse element through omission or commission. As to the influence exerted by the wind-break, this is primarily a matter for measurement by means of instrument, phytometer, and quadrat, both within the community itself and its zone of influence, as well as by comparative determinations outside the latter. Since water relations are of the first significance, the phytometer has a peculiar value in determining the water use of the elements of the wind-break, and of the cultivated and native crops under its protection. Accurate knowledge of the transpiration of the various life-forms and species in all three of these will have a decisive bearing upon the question of possible benefits (Clements, '23).

## RUNOFF AND EROSION

Every agency that destroys the vegetative cover and exposes the surface gives opportunity for erosion and flooding in proportion to the completeness with which it acts. However, all such places constitute initial areas for succession, as a consequence of which the soil again becomes increasingly protected by a series of communities. Such a protective function is peculiarly the property of the subsere, since this is initiated by disturbance on a soil readily susceptible to wear. In the case of typical priseres, on rock or in water, neither medium is capable of erosion and the seral stages are in full control before soil in the usual sense is available. The process is even more completely one of succession than in the projects already discussed and lends itself all the more readily to ecological procedure. It embraces destructive coaction, either progressive or recurrent, at the beginning, with reaction and competition as the forces that bring about increasingly greater control of the surface and upper layer of the soil until the subclimax or climax is attained. The rate and amount of reaction are functions of sere and climax and though they agree in general terms, they differ in detail for

forest, scrub, grassland, desert, and cultivated areas, as they do in lesser degree for the various types of these communities.

Though erosion is usually the most evident of the processes concerned, it is but one of the interactions between climate, vegetation and soil, in which the plant cover is the decisive feature.   The simplest relation is to be seen in erosion by wind, either in dunes where a constant supply of sand is available or in semiarid regions where the soil remains exposed for considerable periods as a result of cultivation, especially in systems with fallow.   When cropping is pushed beyond its proper climatic limits in consequence of a wet phase and economic factors lead to extensive ploughing under and abandonment of fields, the next drought period of the cycle can not fail to bring dust storms, shifting dunes of top soil, and attendant disaster.   In contrast, erosion by water is far less dramatic except in times of torrential floods, but, is much more universal and continuous; the interaction is more complex and the practical methods of control and the results more varied.   It is imperative to take the whole water cycle into consideration to permit a complete analysis and to direct methods and processes to the major objectives.   Thus, while erosion begins only when water acts upon an exposed surface, the intensity, duration, direction, distribution, and nature of the rain are all of significance, and back of these lie the kind of precipitation, whether rain, hail or snow, its relation to season, year, cycle, etc.   Furthermore, it is essential to follow the disposition of the water that falls and hence to measure interception, condensation, transpiration and infiltration by the cover, runoff, evaporation, storage and percolation with respect to soil, and flowage, spreading, impounding and wastage to the sea, as well as in irrigation and urban use.

While cover is the supreme factor in erosion and flooding, its effectiveness exhibits the widest range by virtue of differences in life-form and composition, height, density, root system, and seasonal duration, as well as in the characteristic litter.   In terms of canopy and litter, forest produces the greatest reaction, followed by chaparral and other scrub, while grassland binds the soil with roots as no other community does, though cereal crops naturally approach it in this respect.   Broadleaved forests generally surpass coniferous ones, and deciduous ones are the least effective during the resting season.   However, deciduous foliage transpires more than other types as a rule and reduces the water content correspondingly, while the water loss of grasses is determined by their structure and size, the tall grasses approaching that of deciduous margins and exceeding that of evergreen chaparral. These relations are naturally reflected in the subseres characteristic of the different climaxes and especially of the several types of disturbance.   Fire has a profound effect upon woody communities and the regeneration of the original cover is a slow process, except in such root-sprouting types as the chaparral of California.   If not too frequent, it affects grassland little, but the reaction value of grass may be seriously reduced or almost destroyed by

overgrazing.   In accordance with its completeness, clearing is destructive to all protective reactions, especially in the annual harvesting of many crops, and construction is often but a specialized type.

All the disturbances that affect the protective role of cover are universal in settled regions, but they are most portentous in those with relatively low rainfall, where conservation is the critical need and where recovery of the vegetation, by natural or artificial means, is less rapid and thorough. Floods are more frequent and extensive in humid basins, but their control through vegetation is naturally a much simpler affair.   In the climate and topography of southern California, the number of undesirable events that flow from the burning of chaparral is probably to be equalled nowhere else, when population and productivity are brought into the picture.   Quite apart from the destruction of beauty and of recreation sites, the modified water cycle carries with it material damages of the most serious character. This begins with increased runoff and the accelerated removal of litter and humus, passes into rilling and gullying, flooding and flows of mud and debris, with accompanying disaster to human communities, and ends in the sealing of gravel basins, the silting up of reservoirs, pollution of urban supplies, and enormous losses of priceless water to the ocean.   The re-covering of the denuded slopes by natural succession gradually becomes more and more difficult, transpiration and evaporation are progressively lessened, and the local climate changes for the worse.

In the case of chaparral, as with other root-sprouting dominants and with the rapidly growing fire pines or jack pines, natural recovery regularly ensues in an adequate degree where burning is not too frequent.   The succession in chaparral regularly begins the first winter with an astonishing growth of annual forbs, which usually yield the second or third season to perennials, especially grasses at lower elevations, and these in turn are displaced by the competition of the root-sprouts and seedlings of the shrub dominants after four or five years.   However, along the ranch front, fire may occur too frequently or dry seasons may intervene to retard succession; the terrain may be too steep and rugged for a protective stand, or the buried seeds of forbs or the root-crowns of shrub and bush may be killed by intense fire.

Even more serious is the fact that rain starts in the fall before the annual cover can appear and downpours often occur before this has attained sufficient density to be more or less effective, the situation that caused the tragedy at Montrose in 1934.   In all these cases, nature must be aided and the initial stages of succession hastened and their area extended by sowing. In California, red and black mustard are perhaps unsurpassed in this role and extensive districts have been sown in the Santa Ynez and San Gabriel mountains during the past three years to retard the silting-up of urban reservoirs and to prevent the repetition of disastrous floods.   In this, opportunity has been afforded for comparing sowing by CCC crews and by

airplane in terms of effectiveness and cost, and the quadrat method is also being used for a comparison of natural and artificial succession, as well as the final outcome of the competition between the natives and mustard. Though the entire procedure is still in the experimental stage, the initial results hold much promise for all situations in which rapid recovery is the critical necessity.

Back of all these immediate problems lies the much debated question of the role of cover in general and forest in particular as a source of material for rain or an agency for increasing the local effect. It must be fully recognized that there is no adequate proof that the planting of forests augments rainfall, though some of the supposed instances can not be summarily brushed aside (Zon, '12). However, it can not be gainsaid that deciduous forest in summer may transpire more water per unit area than a body of salt, or fresh water, and hence the hardwoods of the southeast in their virgin condition constituted in rainfall effect an extension of the ocean to several hundred miles inland. This contribution has been decreased by cropping, but the crops of the prairie region transpire in much the same order as the original grasses, a fact that argues strongly against any material increase in the rainfall of the middle west during the period of settlement (Clements, '23). The role of vegetation in providing moisture for local rains is perhaps nowhere more clearly suggested than on Pikes Peak, where convection thunder storms occur at the same general time each day for much of the summer, after the transpiration has reached a certain level determined by the seasonal growth. Conversely, the amount of water transpired represents the toll taken by each type of community for the protection it affords, and this is a matter of prime importance in evaluating the reaction of the various life-forms, tree, shrub, grass, and forb and in different sites, such as climax slope and postclimax canyon floor. For all these reasons, the use of phytometers of the various life-forms concerned is an indispensable feature of the major installations for investigating the water cycle, and these are combined with lysimeters to determine the partition of the water that enters the soil.

While cover and succession must be employed as the major tools in the control of erosion and flooding, it is obvious that engineering works are indispensable complements in many instances, though it is unfortunate that trust has too often been placed in them alone. The more progressive engineers are coming to realize that the proper place to control runoff and erosion is at the start and that check-dams and debris basins are temporary or supplementary devices chiefly needed during the period when the conquest of fire and the restoration of the natural cover are barely under way. Many small check-dams at the heads of small rillways or gullies are far preferable to much larger ones in ravine or barranca, and valuable as debris basins may be in halting or diminishing the momentum of flood materials, it can not be denied that the adequate protection of the native cover will render them unnecessary.

Three general types of measures are employed to determine the amount of runoff and erosion in relation to the several kinds of disturbance and the stages of the natural or artificial succession that ensues. The simplest and most extensive is stream gauging, which possesses the advantage of integrating watersheds of considerable extent, but this is largely offset by the number of variables both in terrain and cover. Watersheds up to at least several hundred acres in size permit closer and more detailed correlation by means of measuring weirs and flumes, especially when topography and vegetation are sufficiently similar to allow installation in triplicate. However, the most intensive measurement can be obtained only from runoff-erosion plots, in which the interaction of cover, water and soil can be traced in minute detail (Lowdermilk, '29, '30, '33). Such plots are essentially transects placed lengthwise of the slope, 2–4 times as long as wide and of such dimensions as to give an area of 100 sq. m., or an aliquot or multiple of it. They are enclosed by a low board wall with an outlet at the bottom into a recording gauge. The plots are arranged in pairs or paired series with a control of the existing cover and such disturbances as are germane to the type, viz., burning, grazing, trampling, denuding, sowing, planting, etc. The course of succession is traced in detail by means of quadrats where these are feasible, or better by a series of overhead views covering all or most of the plot.

## NATURAL LANDSCAPING

The rapid growth of interest in this field has sprung largely from the construction of modern highways in such manner as to accomodate curves and grades to higher speeds, thus requiring more, longer, and deeper cuts and fills. Engineers were apparently entirely unprepared for the effects produced by heavy rains upon the little consolidated fill slopes in particular, and it required a season of supranormal rainfall to supply the needed arguments of harmful mud flows and excessive costs of repair and maintenance to bring recognition of the problem (Kraebel, '34, '35). Here again there was immediate need for a protective cover on loose soil, devoid of germules, and recourse had to be taken to planting and sowing. At the same time, the soil was to be held against the combined action of slipping, slumping and washing, and an initial reaction produced by a terrace supported with stakes and reinforced by wattles (Kraebel, l.c.). This was supplemented by cuttings to carry the binding effect deeper by means of roots and to break the impact of rain by means of crowns, in which procedure *Salix* proved less satisfactory than *Baccharis*, and the reactions were completed by sowing the shelf to one of the grains.

Probably the first organization of guiding principles in natural landscaping and their application on an ecological basis was made in the development of the Blaksley Botanic Garden at Santa Barbara, in which the several climaxes of the region were combined into a consistent treatment in harmony

with the varied topography.    The same idea has been employed in a smaller garden with uniform terrain about the museum in Yosemite Park, and is now in process of being adapted to two California state parks of very different type, namely, Point Lobos near Carmel and Purisima Mission near Santa Barbara.    It has also great possibilities in such restorations as are proposed for the floor of Yosemite Valley, where the original flowery meadows have been entirely dispossessed by weedy grasses, as it does likewise for refuges and reserves of various kinds.    However, its outstanding opportunity lies in the treatment of the Wawona Road between the Valley and the Mariposa Grove.    To reduce the steep grades, this has been carved out of the mountain sides in such manner as to produce a continuing series of cuts for thirty miles, bald and insistent near at hand and forming an unsightly scar from the distance.    These have been organized by sites and units in accordance with terrain and soil, and a detailed plan for preparation and planting worked out for each.    One example of each kind has received the necessary reduction or rounding of slope, with protective trenching above and terracing on the face, and has been sown and planted to yield natural patterns in general harmony with the vegetation present.    The course and outcome of the succession are being followed by tristat and quadrat, and controlled to insure obtaining the effects sought, and these are to serve as the guide for the ultimate landscaping of the entire highway.    In addition, the plan contemplates the enhancement of the original stretches of forest and the many recesses and dells, where soil and water permit installing final compositions without the preliminary successional modification of raw slopes.

Along similar lines, demonstration plantings have been initiated upon several main highways in southern California, where by contrast with mountain roads generally, ornamentation takes precedence over protection, though without neglecting the latter.    In addition to cuts and fills, it is necessary not only to take the entire right of way into account, but also to provide fire protection for the adjoining fields in lieu of the unsightly burning or oiling of the roadside.    The details of this must be left for a projected account of natural landscaping and the ecological principles and methods involved.    The complete plan calls for a unified treatment in which ornamental values predominate, but with adequate attention to erosion control, fire hazard, flow of traffic, and reduced costs of maintenance.    However, the ecologist concerned with the applications of his work may be interested to consider the more important canons laid down.    The chief of these is that nature is to be followed as closely as possible and hence native materials alone are to be employed, preferably from the outset but invariably in the final composition.    While a natural treatment presupposes the use of species and communities in the regional association or faciation, it also permits modification and enhancement consistent within its limits.    The process of succession by which nature reclothes bare areas is to be utilized as the chief tool in landscaping, but the process is often to be hastened or telescoped to secure more rapid and varied results.

## CLIMATE AND CYCLES

To one not accustomed to regarding ecology as a synthesis, it may seem strange that the ecologist should concern himself directly with climate as such, even though the dependence of plants and animals upon physical factors is fully recognized. However, climate and climax are really twin concepts, and the limits of the one can be expressed with fair definiteness only in terms of the other. Climate is in control of the climax and through this of the soil, and it either initiates or circumscribes the varied reactions by which plants mold or control their habitat and in turn influence climate. In consequence, the ecologist is vitally interested not merely in climatic effects, but also in the processes by which these are brought about and in the causes that underlie the latter. His very devotion to changes and cycles in climax and species must be extended to change in the causes concerned and not without the hope that understanding may lead in some measure to anticipation and even the beginning of control.

If further justification for his attitude be needed, it is furnished by the present crisis in the Middle West, in connection with which the question constantly arises even among scientific men as to whether the change is not a permanent one and the country to become a desert. While the answer is a definite and unqualified negative, it is essential to know the grounds upon which this is based. It is equally important though less pleasant to recognize that settlement and cultivation have not increased rainfall, that the winters are not colder and the summers no hotter, and that snowdrifts were not deeper, except relatively, in one's boyhood; in short, that the records prove neither drought nor abundant rain ever comes to stay, but each comes and goes in a more or less definite cycle.

It is at least interesting that renewed activity in the study of climatic cycles should have been focused upon the annual rings of trees as integrators and have developed in close touch with researches on climax and succession (Douglass, '09, '14, '19, '28; Huntington, '14, '25; Clements, '16, '20, '21). From this came further evidence of a probable correlation with the sunspot cycle, its multiples and aliquots, as likewise with the solar constant (Clayton, '20, '23, '26; Abbot, '25, '32, '33). There is now general agreement with Köppen's discovery (1873) that mean temperatures throughout the world are somewhat higher at sunspot minima than at maxima, especially in the tropics. The relation with rainfall is less definite, as well as apparently divergent for certain regions, and agreement upon it is correspondingly less general. In spite of this, an increasing number of investigators in various parts of the world have found more or less correlation, and the chief task at present is to bring the results into general harmony. Because of the critical effect of drought upon both cultural and natural vegetation, the first ecological investigations in the field dealt with the coincidence of drought and sunspot maxima. In these it was shown that a drought period of several years

had occurred in the western United States at each maximum of 80 spots or more, and notably in the early seventies and nineties, accompanied by widespread economic consequences (Clements, '21).

It was logical that this and related hypotheses should be tested by attempts to make long-range forecasts of rainfall some months or even a few years in advance, utilizing chiefly sunspot numbers which themselves permit prediction in general terms, but employing also the solar constant, ocean temperatures, ice indices for the oceans and other criteria. Some of these have achieved considerable if not noteworthy success (McEwen, '18, '34; Clayton, '20; Browne, '25, '29), while the ecological efforts in this field led to the anticipation of the drought of 1917–18 and of the relatively low maximum of 1928 and its indication of no extensive or serious drought. Recent results justify the working hypothesis that sunspot minima are also times of drought, an assumption supported by the prevailingly higher temperatures at such periods and strikingly exemplified by the occurrence of unprecedented drought in the Middle West in 1934–1935. It is unnecessary to point out the significance of long-range prediction for the various projects previously discussed, as well as for the whole social-economic system. Moreover, in spite of the great complexity of the problem, it is fairly certain that the next decade will witness marked progress toward its solution.

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# NOTES ON THE VEGETATION IN THE CUMBERLAND BAY CAVES, MASATIERRA, JUAN FERNANDEZ ISLANDS

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A visitor to Masatierra, the largest island in the Juan Fernandez group, cannot fail to notice, when at anchor in Cumberland Bay, the only harbor in the islands worth mentioning, a series of black patches in the steep sandy slope just east of the landing place (fig. 1). They are the entrances to a number



FIG. 1. The caves in Cumberland Bay, Masatierra.

of caves, some almost filled with sand, others still wide-mouthed as when first dug out. The volcanic rock is very soft, and it cannot have taken much trouble to dig the caves. Tradition tells us that, originally, they were on two levels and that they were excavated by the buccaneers during the 17th and 18th centuries. It is certain that they were used as abodes for political prisoners during the earlier part of the 19th century. I suppose that a study of contemporaneous documents would answer questions regarding their origin and later fate, but as this has little bearing upon our subject, I have not troubled myself with a search for original data.

The lower tier has disappeared altogether due to slides from above and the washing from the rain; and when the wind blows into the harbor from the northeast, it may carry sand from the slopes below into the caves, blocking their entrances, in which barriers of sand are being built up rapidly.

The upper floor contains 10 caves, numbered from east to west I to X, but three of them have disappeared under the sand.

During the last hundred years nobody has occupied these caves except perhaps quite accidentally and for brief intervals. Meanwhile, diaspores of plants have found their way into them. They offer shelter from the wind, a rock forming a soft substratum, constantly high atmospheric humidity, and in some cases also a film of water on the floor, as it percolates down the walls. Two more requirements are necessary to start a vegetation cover: light and plants. Light is very weak in the caves, but so it is in the dense rain forest, and many cryptogams thrive well in the dark and moist recesses and narrow canyons of the woods.

Assisted by my wife I measured and described the caves in 1917 and made a fairly detailed study of the vegetation. Time did not permit a regular series of meterological observations, but in order to afford some comparison of life conditions within and without the caves a normal day was selected on which observations on temperature, air humidity, and light were taken in the caves and outside them as nearly simultaneously as possible. Light was measured with a Wynne exposuremeter.

## The Caves and Their Vegetation

### Cave I

This was small, open and dry, about 2.5 m. high at the mouth and 1.5 m. at the bottom, about 3.5 m. deep and a trifle wider than deep. On the outer 1.5 meters of the floor was a low barrier of sand. Inside this there was a growth of *Histiopteris incisa*, normal and fertile, while behind it, along the slope between the floor and the back wall, where there was more moisture, grew a number of large fertile specimens of *Blechnum auriculatum*. On the walls were solitary specimens of the same species and, lower down, a white sterile lichen. The moisture was apparently not sufficient for most of the bryophytes common in the larger caves; *Balantiopsis lancifolia* alone was noticed, fairly well developed.

### Cave II

This is a large cave, the opening facing ENE and almost blocked by sand, leaving a narrow fissure 16 to 57 cm. high (fig. 2). The height increases rapidly toward the interior, reaching 1.85 m. farthest in. The floor is of fine-grained, moist, sandy clay, plastic only at the foot of the back wall where water seeps in.

On April 3, 10 A.M., the temperature in the inner section of the cave, 180 cm. above the floor, was 19.2°,[1] in the open 21.9°; on the soil surface in the cave 16.3° and in the open 38°. Relative humidity in the cave was 82 per cent, in the open 53 per cent. Light in the cave was 1/310 of the strength outside.

[1] Temperature in degrees centigrade.

The sand heap and the debris at the entrance $f$ had no vegetation.    The inner half was covered with an almost pure *Blechnum* association:
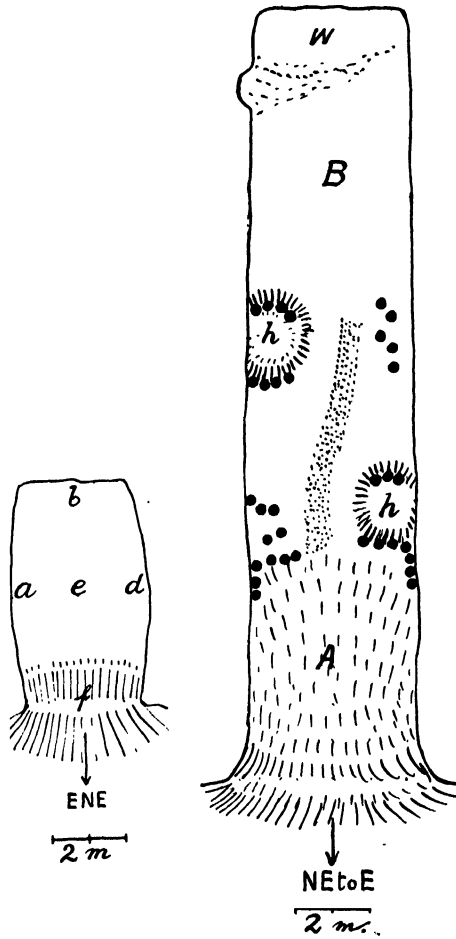


Fig. 2.  Sketch maps of cave II (left) and cave VI (right), $h$, hollows in floor, showing distribution of *Blechnum* (●) facing the entrance; $w$, pool of stagnant water.

F.S.[2]  *Blechnum auriculatum*, soc.
         *Dryopteris inaequalifolia*, sol.
G.S.     *Lepidozia* sp., parc.

The south wall was covered with *Blechnum*. This wall was lighted by the midday sun.    The back wall $b$ and the corners were rather wet and covered

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[2] F.S., indicates field stratum, corresponding to the lower (to 0.2 m.) and middle (0.2–0.8 m.) field strata of Swedish authors. G.S., indicates ground stratum, the appressed cover of the soil.

with algae [3] and moss protonema. The north wall was in the shadow of the sand bank, got less light than any other part of the cave and was practically devoid of vegetation. From the roof in the outer half and in the corner between *a* and *b* a few large specimens of *Blechnum* were found. With the exception of the plants growing near the entrance, *Blechnum* was less fertile than usual, and in the shade of the roof between *a* and *b* the sori became scarce and interrupted.

## Cave IV

Facing NE by N, it is connected with cave V through a narrow passage (not over 1 m. wide) (fig. 3). The entrance, which is 4.2 m. wide, is barred by a bank of debris, leaving an opening 0.55 to 1.1 m. high. Height from floor to roof is 6.2 m. and depth of cave is 16.3 m.
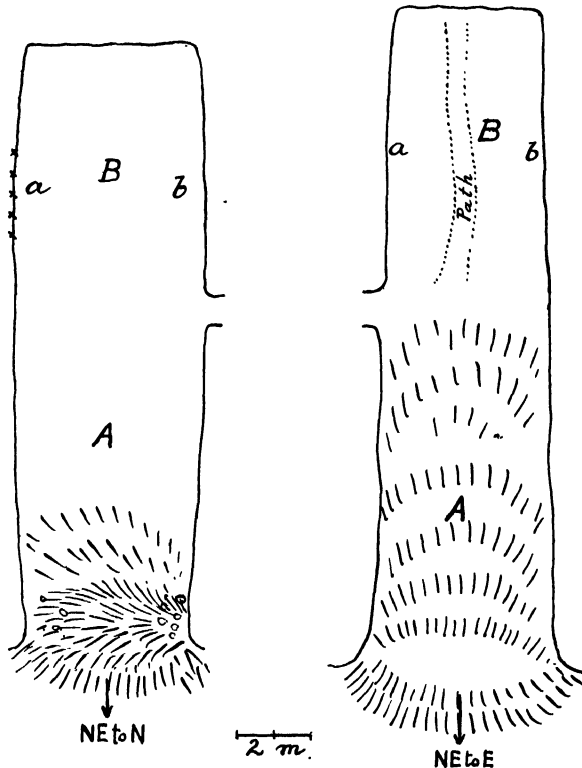


FIG. 3. Sketch maps of cave IV (left) and cave V (right): *a*, south wall; *b*, north wall; *c*, incised letters.

[3] Four or five species of aerial algae were collected in the caves, but unfortunately the list, published in " The Natural History of Juan Fernandez and Easter Island 2 (6): 1922," does not contain any detailed information on their distribution. The species are *Trentepohlia aurea* L., and a form of the same species (?), *Chlorella ellipsoides* Gern. (green slimy patches), *Chlorococcus minor* (Künz.) Naeg., and *Diplonema rupicolum* Borzi.

On April 3, at 6 P.M. temperature 180 cm. above ground was 16.4° at *A* and the same at *B;* on the soil surface it was 16.0° in both cases. Relative humidity in *A* was 86 per cent, in *B* 89 per cent. Light, April 7, 12:30 P.M. was 1/110 at *A,* 1/720 at *B.*

In *A* some specimens of *Blechnum* were found at the foot of the bank; otherwise the soil, trodden hard and smooth, showed nothing but traces of aerial algae. The inner portion *B,* from the passage to cave V down to the back wall, a distance of 6.5 m., was covered with the *Blechnum-Fissidens* association:

F.S.  *Blechnum auriculatum,* sol.
       *Hypolepis rugosula,* sol., rarer than *Blechnum.*
G.S.  *Fissidens maschalanthus,* soc., forming a closed carpet. A few fern
       prothallia were mixed in.
       *Balantiopsis lancifolia,* sol.

The floor was uneven and along the illuminated edges of the shallow pits small plants of *Symphyogyna hochstetteri* were observed.

The limit between *A* and *B* was quite sharp. The floor sloped inward and the moisture became gradually greater until finally the clay could be cut by a knife into thin slices. As the difference in humidity was small, the difference in vegetation was mainly dependent on the light. Unfortunately this could not be expressed in the figures, according to which *A* receives almost seven times as much light as *B.* If the light had been measured on the floor, which in *A,* lies in very deep shade because of the bank across the entrance, this part would have shown less light than *B.*

The walls in *A* had little vegetation, except a pure association of light grayish green *Balantiopsis,* and that only on the north side, as the south was in the shadow of the barrier. *Blechnum,* which occurred scattered, reached to the intercave passage, but did not go as far on the south wall. The higher parts of these walls lay in deep shadow and had no macroscopic vegetation, only well developed pure associations of algae, to judge from the color, mainly *Trentepohlia.* This growth continued into *B.* Here the walls showed a poorly developed *Blechnum-Fissidens* association, with much *Balantiopsis* and with more *Symphyogyna* than on the floor. The influence of the light was clearly shown on the south wall. A line of large letters had been cut in the wall (x in fig. 3). They were not visible from the back wall but from the opposite side they shone out bright green, because the edge facing the entrance was densely covered with *Symphyogyna* and green algae, while the opposite margin, always in darkness, was devoid of vegetation. The upper portion of the back wall lay in darkness and showed only the same *Trentepohlia* association as before. Below it was a well developed *Symphyogyna hochstetteri* association with *Fissidens* mixed in. The field strata were represented by few feeble specimens of *Blechnum* and *Hypolepis.*

## Cave V

There is only a low entrance barrier, about 0.5 m. high, so that the opening measures 2.5 m. in vertical and 5.3 m. in horizontal dimensions. At the connecting passage the width of the cave is 4.25 m.; at the back wall, 3.9 m. Halfway the height is 3 m., but from there the floor slopes so that the height of the room increases to 6.2 m. at the back wall. The length of the floor is 18.1 m. (fig. 3).

Observations made April 3, at 2:30 P.M. gave temperature 180 cm. above ground at $A$ 17.1°, at $B$ 16.4° and outside the case 17.6; at surface of soil, at $A$ 17.5°, at $B$ 15.1° and in the open 27.9°. Relative humidity in $A$ 82 per cent, in $B$ 89 per cent, and outside the cave 66 per cent. Light in $A$ 1/6 and in $B$ 1/34; April 7, at 12:30 P.M., light 1/35 in $A$ and 1/260 in $B$.



FIG. 4. Interior of cave V showing path and *Hypolepis* on either side: on the wall to the right *Hypolepis* below and *Blechnum* above and at the rear. Photo by K. Bäckström.

$A$ was covered with debris, and solitary specimens of *Blechnum,* and, on the outside of the barrier, of *Aira caryophyllea* and *Rumex acetosella* were

observed.   In *B* there was a well trodden path running down to the back wall, and a more intact surface on each side of it.   The path was covered with *Fissidens maschalanthus* forming an almost pure association, only a few *Symphyogyna* and *Balantiopsis* being mixed in.   On both sides was a well developed *Hypolepis-Fissidens* association (fig. 4).

F.S.    *Hypolepis rugosula,* cop.
        *Blechnum auriculatum,* sol.
        *Pteris berteroana,* sol. (small, sterile).
        *Aristotelia maqui,* 2 seedlings.
G.S.    *Fissidens maschalanthus,* cop.
        *Symphyogyna hochstetteri,* parc.
        *Balantiopsis lancifolia,* sol.

On the side walls in *A* little grew except the *Trentepohlia* association, a few plants of *Blechnum* and small mats of *Bryum* sp.   The *Trentepohlia* cover continued into *B,* but bryophytes soon became more important.   The difference between the south and north wall in *B* was expressed in the distribution of the ferns.   There were scattered fertile specimens of *Hypolepis* on the south wall; on the north they were replaced by *Blechnum,* which was abundant here, while, except close to the floor, there were only a few small specimens of *Hypolepis,* which apparently needs more light than *Blechnum* to thrive well.   Towards the interior the ferns became much more scarce, especially *Hypolepis; Blechnum* was able to advance much farther in.   In the corner with *Blechnum, Trichomanes* was found.   The upper part of the back wall never reached by the sunlight, unfortunately, was out of our reach, but to judge from its color and general appearance, it was covered with the same *Balantiopsis-Fissidens-Riccardia* association as lower down, where it could be studied.   *Trentepohlia* and *Chlorella* in patches alternated with *Riccardia,* mostly *R. breviramosa,* but also with some *R. insularis* and *Symphyogyna.* They formed a carpet as wet as a sponge.   Large patches of yellowish, dead *Riccardia* could be peeled off, and under them a new cover was forming.   The field stratum was represented by *Hypolepis* in the south and by *Blechnum* in the north section of the wall.   This was the wettest portion, with the following *Blechnum-Riccardia* association:

F.S.    *Blechnum auriculatum,* cop.
        *Hypolepis rugosula,* sol.
G.S.    *Trichomanes exsectum,* sol.
        *Riccardia breviramosa,* soc.
        *Fissidens maschalanthus,* cop.
        *Balantiopsis lancifolia,* parc.-cop.
        *Riccardia insularis,* parc.
        *Symphyogyna hochstetteri,* parc.
        *Distichophyllum subelimbatum,* greg., several small areas
        *Philonotis krauseana,* parc.
        *Lepidozia* sp., sol.

## Cave VI

The entrance faces NE by E. The sandy barrier is low, the opening being 2.5 m. high and 5.6 m. wide, rapidly narrowing to 4.4 m., which width is kept all the way back (at back wall 4.1 m.) (fig. 2).

Observations made April 3, at 2:40 P.M. gave the temperature 180 cm. above ground in *A* 17.1°, in *B* 15.8° and outside the cave 17.6°; on surface of soil in *A* 16.2°, in *B* 15.0° and outside 27.9. Relative humidity in *A* 72 per cent in *B* 93 per cent and in the open 66 per cent. Light in *A* 1/7, in *B* 1/50; April 7 at 12:30 P.M. light 1/30 in *A* and 1/270 in *B*; at the back wall 1/540.

The floor was a reddish brown, hard clay, as a rule wet, at least in *B*. There were, as usual, some *Blechnum* along the foot of the barrier; besides two strangers to the caves were listed, one plant of *Erigeron fruticosus* and one of *Cyperus vegetus*. The outer half of *B* was covered with the *Blechnum-Fissidens* soc. Both plants always turn their fronds so that they get the full
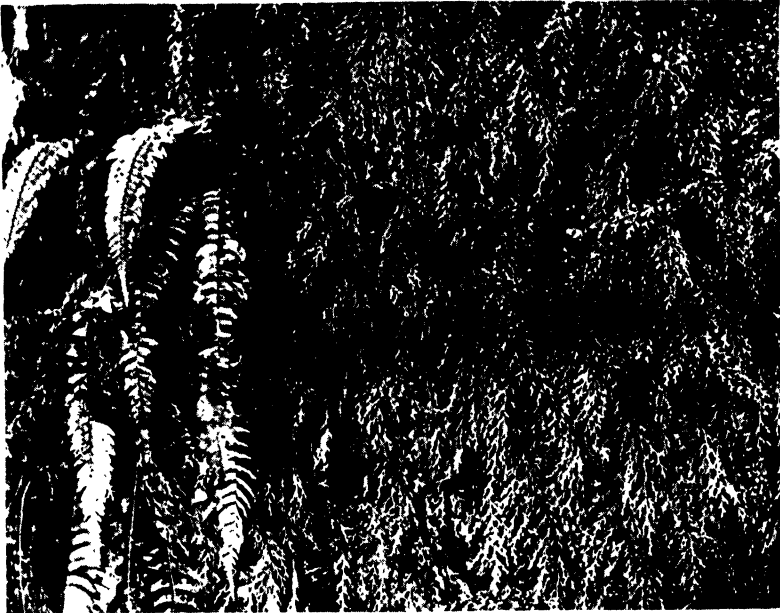


FIG. 5. *Trichomanes exsectum* on back wall of cave VI. To the left *Blechnum auriculatum*. Photo by Skottsberg.

measure of the light available. The farther we advance, the more frequent *Riccardia breviramosa* became, and with it are associated *Balantiopsis, Symphyogyna* and *Philonotis*. It soon became too wet for the ferns, and near the back wall was a pool of water.

The walls in *A* were devoid of a closed cover and showed only scattered specimens of *Blechnum*. In *B* both sides were rather alike; a vertical surface near the corner was covered with a *Blechnum-Trichomanes-Fissidens* association.

F.S.2.  *Blechnum auriculatum*, parc., large and well developed.
F.S.1.  *Trichomanes exsectum*, soc.
      *Dryopteris inaequalifolia*, sol., sterile.
G.S.  *Fissidens maschalanthus*, soc.
      *Symphyogyna hochstetteri*, cop.
      *Riccardia breviramosa*, cop.
          "     *insularis*, sol.
      *Distichophyllum subelimbatum*, sol.[4]

The back wall showed the same association on vertical surfaces, and I have never observed a finer growth of *Trichomanes* than in this place; it luxuriated in vegetative respect and was still fertile (fig. 5). A portion of the wall sloping about 80° was free from *Trichomanes*, perhaps being too wet, and was covered by a pure bryophyte association, with *Fissidens* and *Riccardia breviramosa* as leading species.

From the roof scattered plants of *Blechnum* hung down; they were more numerous in *A* than in *B*.

## Cave IX

A small shallow niche, dry and half filled with sand. On the back wall and hanging down from the roof were a few specimens of *Blechnum*.

## Cave X

Only an open niche left, considerably wider than deep. In hollows in the walls grew solitary specimens of *Blechnum, Histiopteris, Polystichum berterianum, Rumex* sp., and *Verbena litoralis*.

### LIST OF SPECIES FOUND IN THE CAVES

#### *Flowering plants*

All these were rare, occurred in the outermost portion and do not belong to the genuine cave flora.
*Aira caryophyllea* L. Cave V.—A weed.
*Aristotelia maqui* L'Hérit. Cave V. Two seedlings.—A large shrub and a very dangerous weed.
*Cyperus vegetus* Willd. Cave VI, 1 ind.—Perhaps indigenous.
*Erigeron fruticosus* DC. Cave VI, 1 ind.—Rocky places both near the sea and up on the ridges. Endemic.
*Rumex acetosella* L. Cave V.—A weed.
*Rumex* sp. Cave X.—A weed.
*Verbena litoralis* Kunth. Cave X.—A weed.

#### *Ferns*

*Blechnum auriculatum* Cav. In all the caves the commonest vascular plant, and one of the commonest plants in the islands, both in the forests and in

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[4] *Balantiopsis lancifolia*, not collected or noted, was probably also there.

the open, represented by sun and shade forms. The most pronounced shade forms are found in these caves.

*Dryopteris inaequalifolia* (Colla) C. Chr. Cave II, rare; cave VI, scattered on the walls.—A common forest fern, also in more open situations. Endemic.

*Histiopteris incisa* (Thbg) J. Sm. Caves I and X.—Not uncommon in the basal forests and quite frequent in some of the deforested valley bottoms.

*Hypolepis rugosula* (Labill.) J. Sm. var. *poeppigii* (Kze) C. Chr. Cave IV, on floor; cave V, abundant on the floor, scattered on the walls.—Lower forests, not common.

*Polystichum berterianum* Roth emend. Schott. Cave X.—Common in the basal region on sunny slopes. Endemic.

*Pteris berteroana* Ag. Cave V.—An important forest species, especially in the montane region.

*Trichomanes exsectum* Kze. Caves V and VI.—Here and there in wet montane forests.

## Mosses

*Bryum* sp. Cave V, on wall.

*Distichophyllum subelimbatum* Broth. Caves V and VI, wet areas on walls. —Upper montane rain forest, with *Dicksonia*, etc. Endemic.

*Fissidens maschalanthus* Mont. The special cave moss, very common in caves IV, V and VI.—Wet soil in rain forest, moist rock walls etc., on both islands. Endemic.

*Philonotis krauseana* C.M. Cave V, very wet places on back wall; cave VI, on floor in *B*.—Streams, both islands, rare.

## Hepatics [5]

*Balantiopsis lancifolia* Steph. Caves I, IV, V, VI, abundant in IV and V, forming pure patches of a dull grayish green hue. On trees in the rain forest. Endemic.

*Lepidozia* sp. (Close to *L. disticha* Steph.) Caves II and V. An endemic species.

*Riccardia breviramosa* (Steph.) Evans. Very abundant in caves V and VI, especially on back wall.—Wet forest on both islands. Endemic.

*Riccardia insularis* Schiffn. Caves V and VI, on wet walls, less common than the former.—Not known outside the caves. First described from St. Paul and New Amsterdam Islands in the southern Indian Ocean, the only other localities known.

*Symphyogyna hochstetteri* Nees et Mont. Caves IV, V and VI, rare on floor, not uncommon on the walls, very abundant in cave VI.—Not rare in rain forest on both islands. Outside Juan Fernandez only found in the Falkland Islands.

[5] I am indebted to Professor A. W. Evans for the determination of the Hepaticae.

## SUMMARY OF OBSERVATIONS

Only caves II to VI are considered here. Except in II, which is not very deep, we have distinguished between an outer portion *A* and an inner *B*. The former is drier, both soil and air, and slightly warmer. It is also lighter, as shown by a comparison between the light figures for *A*, 1/6 to 1/110 as compared with *B*, 1/35 to 1/720.

With respect to their capacity of enduring shade the ferns arrange them-selves in a series *Polystichum—Histiopteris—Pteris—Dryopteris—Blechnum —Hypolepis—Trichomanes;* only *Trichomanes* is an obligate shade species which has found ideal conditions in the dark, moist and sheltered caves.

All the bryophytes were represented by shade species, and consequently they thrive in the dark wet recesses of the caves, being well developed on the back walls and in the inner corners. *Balantiopsis, Fissidens* and *Symphyo-gyna* have the widest amplitude and also do well a little farther out, if mois-ture is sufficient. They are less exacting as regards moisture in which respect the series would run as follows: *Balantiopsis—Fissidens—Symphyogyna— Distichophyllum—Philonotis—Riccardia.* The last two luxuriate where the water trickles down on them. With decreasing light and increasing moisture the three principal cave associations are: *Hypolepis—Fissidens, Blechnum— Fissidens, Trichomanes—Fissidens—Riccardia.* At times the ferns may be missing leaving pure bryophyte associations.

## ORIGIN OF THE CAVE FLORA

With one exception all the species of the caves are found also in other places in the islands. All have light spores which may be carried great dis-tances. The caves, however, face the sea, and with the prevailing wind di-rection—winds other than SE—S—SW. are rare—nothing is carried directly into the caves, but the wind from the sea may bring back very light diaspores suspended in the air, like the spores of ferns and bryophytes. The entire cave flora may have originated in this manner, but more likely man has acted as the agency in many cases, transporting spores and fragments of thalli from one cave to another. The result has been a series of natural plant associa-tions grouped according to external conditions. New arrivals and a change in the conditions may affect the present equilibrium. The survey of the caves should be repeated some time in the future.

The exception referred to above is *Riccardia insularis* which appears to have its single station on the islands in the caves, from which we should not, I think, draw any far-reaching conclusions. It is hardly probable that it has travelled directly from St. Paul or New Amsterdam to Masatierra after the caves were dug; it is much more likely that it belongs to the indigenous flora but has escaped the attention of collectors.

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# SERE, CLIMAX AND INFLUENT ANIMALS WITH SPECIAL REFERENCE TO THE TRANSCONTINENTAL CONIFEROUS FOREST OF NORTH AMERICA[1]

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## CONTENTS

## I. INTRODUCTION

Plant ecologists have regarded an essentially complete difference in climax dominants as the basis for the recognition of the major plant communities called plant formations. This viewpoint is brought out clearly in the separation of the pine-hemlock or lake forest from the northern coniferous forest (Weaver and Clements '29), and perhaps not less clearly by the separation of the subalpine forest from the montane forest. In no instance known to the writers have animals been considered as indicators. The recognition of formations solely on plant evidences is in accord with the general views and practices of the plant ecologist.

The associations which constitute a major community (biome or formation) usually include some wide-ranging species among the dominants. These constitute the element of unity in the climax portions of the formation and tie the several associations of the formation together. It is the purpose of this paper to show that it is not always feasible to make sole use of the criteria of plant dominants and maintain the integrity of some of the impor-

tant natural units in a bio-ecological system of classification. The biome or bio-ecological formation is based upon both plants and animals. Bio-ecology considers that plants and animals are inseparably united in the structure of any community. One purpose of this paper is to point out some hitherto unrecognized relations of the really potent animals of the northern coniferous forest to the seral stages and to the plants of lesser importance, from the viewpoint of climax.

## II. Unity of the Biome and Evaluation of its Constituents

In this treatment, animals conceived of as "influents" are defined as animals having very obvious effects on the plants or animals of the community and on the habitat. Major influents are large potent animals; minor influents have lesser effect and are usually smaller.

Various influents range over and make use of the climax and of the seral stages, thus covering most of the subordinate community types and subordinate habitats included in the biome. Ranging influents may be called permeants.[2] Permeant major and permeant minor influents may be recognized; they may stay within less than 10 miles of their original homes, but range through all the available seral stages nevertheless.

The large ungulates and carnivores are major influents and the smaller animals such as the groundhog and the various seed and bud eating birds have lesser effects and are classified as minor influents. Climax influents are largely confined to the climax, etc. Few animals which might be called subinfluents are mentioned. The use of the terms major and minor influents may be justified in some degree by the fact that most ecological studies are conducted in areas where the major and minor influents have been largely eliminated by man's activities, in such areas the term "influent" has been applied to the more potent of the very small animals such as insects and subinfluents to the less potent ones. These have usually been treated as influent and subinfluent without reference to the more important large ones referred to in this paper as major and minor influents.

Three subdivisions or associations of the transcontinental coniferous forest (*Picea-Pinus* biome[3]) (fig. 1) are considered, with respect to relations of the various animals to the climax and seral stages as follows:

1. Pine-hemlock (*Pinus-Tsuga*) association, located in the Great Lakes region.
2. Spruce-balsam fir (*Picea-Abies*) association, extending from the Atlantic to the crest of the coast mountains and south to about 55° in the Rockies.

[2] Wandering widely.

[3] Names of biotic communities should include animals but these are withheld pending further study of the montain forest communities of the United States. For the transcontinental forest *Picea-Pinus-Alces*, spruce-pine-moose, is appropriate, but if the mountain forests are included, the most widely distributed climax coniferous trees with lynx would be appropriate (see fig. 11 and p. 389).
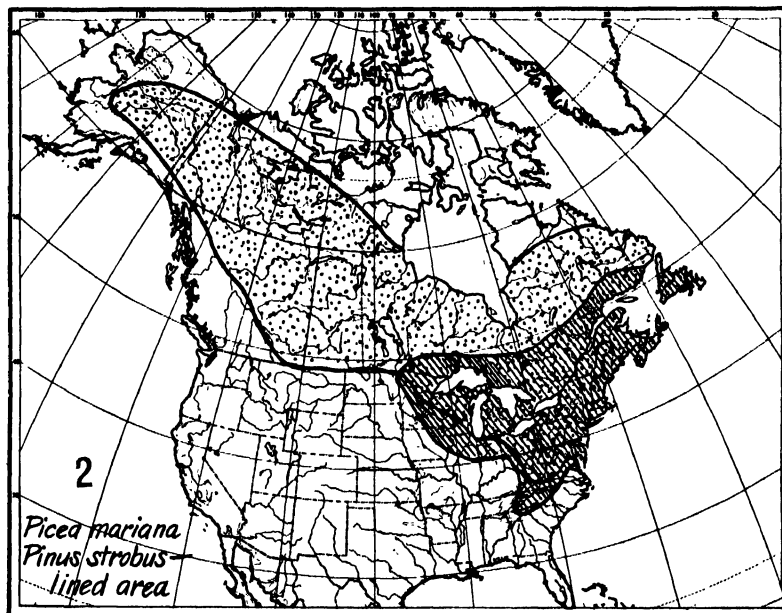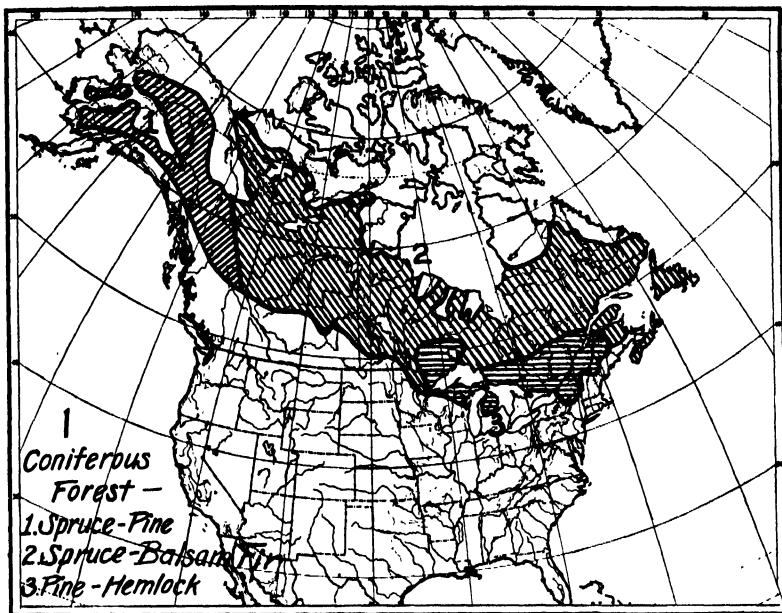
FIG. 1.   The location of the three associations in the transcontinental coniferous forest.

FIG. 2:   The distribution of one climax dominant the *Pinus strobus* and one important generally distributed subclimax dominant, the *Picea mariana*.   Compare with figure 1 for extensions of range outside of the coniferous forest where dominance is of outstanding importance.   Outside areas of dominance, these trees occur in small scattered groups, separated by miles of deciduous forest or grassland.

3. Spruce-pine (*Picea-Pinus*) association, in the interior valleys of northern British Columbia, the Yukon, and Alaska.

In the spruce-pine (Alaskan) area, the unity of the formation is shown by the continuous range of the climax dominant, white spruce, and by the late subclimax dominants, black spruce, aspen, balsam poplar, and paper birch. The influent animals of the spruce-pine show considerable differences when compared with the transcontinental and Great Lakes areas, though several binding species are present.

In the Great Lakes areas, the biome unity is given very largely through the influent animals and subclimax plants. The pine-hemlock climax is quite distinct as regards climax dominant plants. The spruce-balsam fir association, embracing the transcontinental area, possesses the unifying plant dominants and animal influents of both the other associations to a greater degree than the other climaxes, and should be considered as a representative section of the biome. The three climaxes resemble each other in both animal and plant characteristics.

Climax and late subclimax dominant plants enumerated below are common to two or more of the associations, the subclimax species occurring frequently as minor relics in the climax are starred. The numbers refer to animals feeding on them, see tables I to V, pp. 383, 391, 392, 393 and 394. The plants indicated by unmarked numbers and all plants not bearing specific numbers have been observed by the junior author to be used by herbivorous species listed in the tables. The symbols on the other numbers signify that the information is from the following sources: * A. C. Twomey, Alberta (Personal communication); † Dugmore ('13), Newfoundland; ‡ Seton ('07), Great Slave Lake; § Osgood ('00, 04, 07, 09), Alaska and Yukon; || Dice ('20, '21), Central Alaska; ¶ Swarth ('22), British Columbia; ** Grange ('32), Wisconsin; ( ), plant listed in habitat but feeding not mentioned.

> *Picea glauca,*[4] white spruce (fig. 9), 20||, 61, 61||, (64), 65, 68.
> *Abies balsamea,* balsam fir (fig. 9), 24**, 61, (64), 65, 66, 67.
> *Larix laricina,* larch, 24**, 51, 61.
> *Picea mariana,* * black spruce (fig. 2), 24**, 51, (64), 65, 68.
> *Pinus banksiana,* jack pine, 24**, 53, 61, 71.
> *Populus tremuloides,* aspen.
> *Populus balsamifera,* * balsam poplar.
> *Betula papyrifera,* * paper birch, 24**.

The white spruce gives unity to the transcontinental and Alaskan divisions. The climax binding dominants are wanting in the pine-hemlock area and unity is indicated by the starred species only.

[4] Nomenclature of trees follows Sudworth's "Check list" and that of other plants Gray's "New Manual." All authors' names are omitted. Scientific names are given usually only in the first mention of the species.

### A. Similarity of the Subclimaxes

Subclimaxes can be divided into xerosere and hydrosere. The following associes are typical and distributed throughout the entire biome. The groupings are separated by lines and ♯ indicates that the species may be absent.

Xerosere, includes the following groupings:

a. Paper birch, white spruce♯, and quaking aspen♯.

b. Balsam fir♯, jack pine, and quaking aspen♯.

c. *Juniperus* sp., juniper, 32, 40;[5] *Corylus* sp., hazel, 1, 2, 61; *Rhus* sp., sumach.

d. *Cladonia* spp., lichens 3, 4§; *Vaccinium* spp., blueberry.

In the Alaska area, the jack pine is replaced by the *Pinus contorta*, lodge-pole pine, and the balsam fir by *Abies lasiocarpa*, alpine fir.

Hydrosere, includes the following groupings:

1. Late subclimaxes.
   a. Black spruce, 51; larch, 52; *Fraxinus nigra*, black ash♯; *Thuja occidentalis*, white cedar♯, 24.
   b. *Alnus* sp., alder, 1\*, 20‖, 20§; *Salix* spp., willow, 1\*, 2¶, 2‖, 19\*, 22\*, 22‖; *Betula* spp., dwarf birch, 1\*, 2‖, 25§.

2. Early subclimaxes.
   a. *Ledum groenlandicum*, labrador tea; *Chamaedaphne calyculata*, leather-leaf; *Andromeda polifolia*, wild rosemary; sphagnum.
   b. *Carex aquatilis*, *C. lenticularis*, *C.* spp., sedges, 1, 2; *Kalmia polifolia*, swamp laurel.
   c. *Scirpus hudsonianus*, cotton grass, 21, 22, 23, 24; *Zizania aquatica*, wild rice, 1, 2, 46, 47.
   d. *Castalia odorata*, water lily, 1, 2, 46, 47; *Potamogeton alpinus*, pondweed, 1, 2.
   e. *Chara* spp.; *Myriophyllum* spp., 1, 2; *Potamogeton* spp., 1, 2.

The subclimaxes resemble each other in the different parts of the biome through the occurrence of the following dominants or subdominants.

The binding dominants and subdominants existing under similar physical conditions are as follows:

Dominant trees, xerosere.

*Populus tremuloides*, aspen, 1, 1\*, (2), 3, (4), 21, (22), (23), 24, 19, 20, 32.

*Populus balsamifera*, balsam poplar, 1, 1\*, (2).

*Betula papyrifera*, paper birch, 1, (2), 3, (4), 19, 21, 22‖.

Subdominants.

*Prunus pennsylvanica*, pin cherry.

*Prunus virginiana*, choke cherry, 3, (4), 11, (12), 13, 18, 61.

[5] Numbers indicate the animals which eat the plant or its seeds. See tables I, II, III, IV, V.

*Acer spicatum*, mountain maple, 1, 2, 3, 4.
*Acer pennsylvanicum*, striped maple, moosewood, 1, (2), 3, (4).
*Corylus rostrata*, hazel, 61, 62.
*Corylus americana*, hazel, 3, 4, 61.
*Vaccinium vitis-idaea*, mountain cranberry.
*Lathyrus palustris*, swamp vetchling, 1, 21, 3.
*Lathyrus venosus*, everlasting pea, 1, 21, 3.
*Lathyrus ochroleucus*, everlasting pea, 1, 21, 3.
*Amelanchier alnifolia*, service berry, 3, (4), 11, 18, 32.
*Viburnum opulus*, highbush cranberry, 4a†.
*Juniperus horizontalis*, prostrate juniper, 32, 40.
*Juniperus sibirica*, juniper, 32, 40.
*Juniperus communis*, juniper, 32, 40.
*Diervilla lonicera*, bush honeysuckle.
*Rosa acicularis*, wild rose, 11, 18, 32, 61.
*Rubus strigosus*, bramble, 11, (12), 13, 61.
*Empetrum nigrum*, crowberry, 3, 4.
*Arctostaphylos uva-ursi*, bearberry, 3, (4), 11, (12), 13, 32.
*Vaccinium canadense*, blueberry, 3, (4), 11, (12), 13, 32.
*Ribes* spp., currant and gooseberry, 11.
*Symphoricarpos racemosus*, snowberry, 11, (12), 13, 32.
*Vaccinium* spp., huckleberry, 11, (12), 13, 32.
*Cornus canadense*, bunch berry, 32.
*Cladonia* spp., caribou moss, 3, 4§.
*Rubus* sp., blackberry, 11, (12), 13.
*Actaea alba*, baneberry, 11.
*Rubus* sp., raspberry, 11, (12), 18.
*Shepherdia canadensis*, buffalo berry, 11, (12), 13.

Dominant trees, hydrosere.

*Picea mariana*, black spruce, 51, 52.
*Larix laricina*, larch, 52.
*Thuja occidentalis*, white cedar (local), 24**.

Subdominants, shrubs.

*Betula pumila*, dwarf birch, 24**.
*Betula glandulosa*, dwarf birch, 2§, 25‖.
*Betula glandulifera*, dwarf birch, 1, (2), 3, (4), 27, (23), (22), 24, 24**.
*Alnus incana*, speckled alder, 1, (2), 3, 4a†, (22), (23), 24, 24**.
*Salix candida*, willow, 24**.
*Salix longifolia*, willow, 24**.
*Salix reticulata*, willow.
*Salix discolor*, willow, 1, (2), 3, 4a†, 21, (22), (23), 24.
*Sorbus americana*, mountain ash, 1, (2).
*Cornus stolonifera*, red osier dogwood, 3, (4).
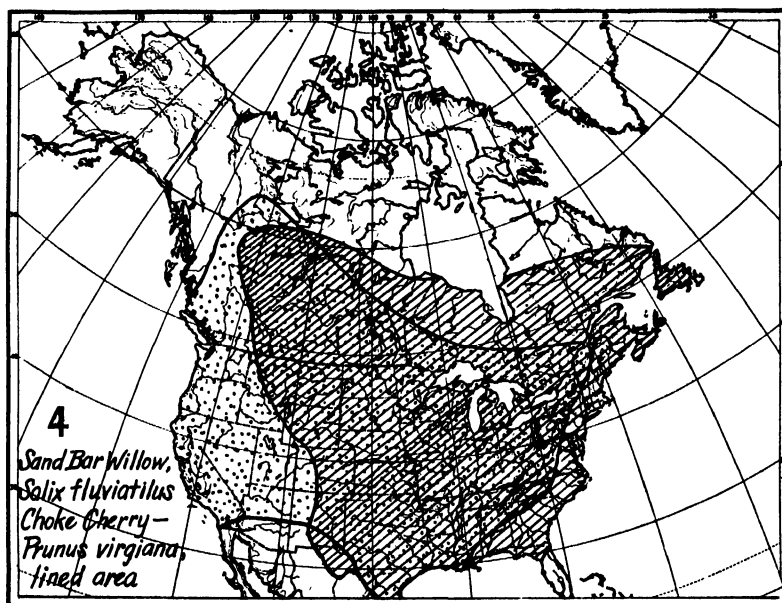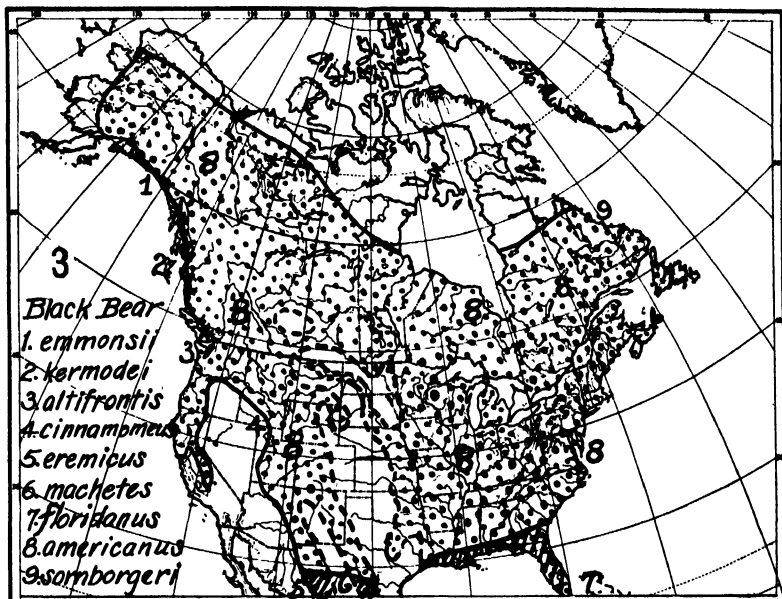
FIG. 3. The distribution of the black bear (*Euarctos americanus*) showing an unusually extensive range. The varieties are dispersed among the typical form; the generally recognized species are shown by a different legend. In general the distinct species, 3 or 4 in number, occupy the lined area in the southeastern United States and northeastern Mexico. *E. kermodi* is also probably a distinct island species. (Modified from Seton; nomenclature after Seton.)

FIG. 4. The distribution of two wide ranging plants. No great number of subspecies has been recognized. Compare with figure 3.

*Andromeda polifolia*, wild rosemary.
*Chamaedaphna calyculata*, leather leaf.
*Ledum groenlandicum*, labrador tea.
*Ledum palustre*, labrador tea.
*Kalmia polifolia*, swamp laurel.
*Kalmia angustifolia*, swamp laurel.
*Kalmia latifolia*, swamp laurel.
*Vaccinium uliginosum*, blueberry, 3, (4), 11.
*Lonicera oblongifolia*, swamp honeysuckle.

Subdominant herbs (These give unity only in *combination* with each other and additional plants, which characterize the coniferous forest).

*Scirpus hudsonianus*, alpine cotton grass.
*Zizania aquatica*, wild rice, 46, 47.
*Carex aquatilis*, sedge, 46, 47.
*Carex lenticularis*, sedge, 1, 21, (22), (23), 24.
*Eriophorum gracile*, cotton grass.
*Eriophorum angustifolium*, cotton grass.
*Equisetum fluviatile*, horsetail, 1, 2‖.
*Typha latifolia*, common cattail.
*Typha angustifolia*, cattail.
*Usnea* spp., old man's beard on larch and spruce, 3, (4).
*Arisaema triphyllum*, indian turnip, 11.
*Calamagrostis hyperborea*, reed bent grass, 21, (22), (23), 24.
*Calamogrostis langsdorfii*, reed bent grass, 1, (2).
*Agropyron caninum*, wheat grass, 1, (2), 21, (22), (23), 24.
*Nymphaea advena*, yellow water lily, 1, (2), 4a†.
*Castalia odorata*, white water lily.
*Castalia tuberosa*, white water lily, 1, (2).
*Calla palustris*, water arum.

The typical dominants and subdominants of the various subclimaxes characteristic of the northern coniferous forest mentioned above are found either as those species or equivalent races throughout the three associations. The fact that they range more or less uniformly throughout the entire biome in characteristic combinations tends to impart a definite unified characteristic to all of its seral stages. Subclimax vegetation in Alaska or the Athabasca-McKenzie region does not differ greatly, therefore, from subclimax vegetation in Ontario or Quebec.

A characteristic feature of the northern coniferous forest in the present age is that the areas of pure climax are relatively limited in size while the subclimax areas make up the greater part throughout its entire range. This fact tends to impart to the coniferous forest a decidedly subclimax characteristic in which the seral stages become unifying elements along with the climax stages themselves.

## III. The Biome as Viewed from the Standpoint of Coaction and Reaction

### A. Major Permeant [6] Influents

*Occurrence in the climax and seral stages.* The animals of any biome under primeval conditions include a series of major influents. These are the large animals, especially the large ungulates which destroy large quantities of plant materials, tramp the soil, influencing in one way or another the vegetation upon which they depend for sustenance. Preying upon the major influent herbivores are certain major influent carnivores. One of the outstanding characteristics of the major influents is that they range over the climax and subclimax stages of the entire biome.[7]

TABLE I. *Major permeant influents in the different forest associations.**

| | Des. | SB | PH | SP |
|---|---|---|---|---|
| *Alces americana* (Clinton),[8] eastern moose | 1 | x | x | |
| *Alces gigas* Miller, Alaska moose | 2 | | | x |
| *Rangifer caribou caribou* (Gmelin), woodland caribou | 3 | x | x | |
| *Rangifer osborni* Allen, Osborn's caribou | 4 | | | x |
| *Rangifer terraenovae* Bangs, Newfoundland caribou | 4a | p | | |
| *Canis lycaon* Sch., gray wolf 1, 3, 4a, 21, 24, 23 | 5 | p | p | |
| *Canis nubilus* Say., gray wolf 1, 21, 24 | 6 | p | p | |
| *Canis occidentalis* (Rich.), Alaska gray wolf 22 | 7 | p | | p |
| *Lynx canadensis canadensis* Kerr., Canada lynx 21, 22, 23, 46, 61, 20 | 8 | x | x | x |
| *Lynx canadensis mollipilosus* St., arctic lynx 22, 46, 61, 20 | 9 | | | p |
| *Lynx subsolanus* Bangs, Newfoundland lynx | 10 | p | | |
| *Euarctos americanus americanus* (Pal.), black bear | 11 | x | x | x |
| *Ursus alascensis* (Mer.), Alaska grizzly | 12 | | | x |
| *Ursus horribilis* Ord., grizzly bear | 13 | p | | |
| *Gulo luscus* (Linn.), wolverine | 14 | x | x | x |
| *Bubo virginianus subarcticus* Hoy, arctic horned owl | 15 | p | x | x |
| *Bubo virginianus heterocnemis* (Ober.), Labrador horned owl | 16 | p | | |
| *Vulpes rubicosa* Ban., Nova Scotia red fox | 17 | p | | |
| *Vulpes fulva* (Des.), red fox | 18 | x | x | |
| *Vulpes alascensis alascensis* Mer., Alaska red fox 22, 61, 20 | 18a | | | x |

* Headings of column have the following meaning: Des.; Numbers are used in the plant lists on pp. 378, 379, 380, and 382 to indicate the animals eating the plants or their seeds. In the column with common names they indicate the animals eaten. For numbers above 18 see succeeding tables. SB, Spruce-balsam fir association; PH, Pine-hemlock association; SP, Spruce-pine association.

    x indicates that the animal is found throughout most of the association.

    p indicates that it is restricted to a portion of the association.

    [6] Wandering widely.

    [7] In considering these, it is necessary to recognize that there are two types of species and subspecies; (*a*) those that have special habitat relations, showing that the development of new habit has accompanied the differentiation of races, and (*b*) those that have specific differences but no differentiation in habitat relationships. Either the race becomes mixed with the general population in all or part of the habitat, or occupies a portion of it as an equivalent species.

    [8] The nomenclature of the mammals follows Miller's check list, that of the birds follows the A. O. U check list. Authors' names are not given for birds.

*Coactions—use of the climax and subclimax plants by the major permeant influents.* The moose is represented by two species equivalent as to general habits and coactions. *Alces americana*, ranging from the Atlantic to the western mountains and occurring in the pine-hemlock and spruce-balsam fir associations, and *Alces gigas*, occurring in the northwest where it occupies the pine-spruce association (fig. 5, 7, 8; Osgood, '07). The use of the plant cover by the moose for shelter and food, especially in the winter, includes (*a*) climax stands of such dominants as white spruce, balsam, red and white pine and (*b*) subclimax stands of jack pine, aspen, birch, and black spruce.[9] Most of its relations in the spring, summer and early autumn, however, are to the early seral stages for during these periods, much of the food is the white and yellow water lilies, sedges and grasses, pondweeds (fig. 7), the twigs of willow, alder (Seton, '11), birch, aspen (fig. 8), and some equisetum. Of all the hydrosere dominants and subdominants, the black spruce is the only one which can be said to provide shelter only.

The moose finds shelter and food in the xerosere when it is forced away from its spruce swamp and bog habitat by the approach of cold weather. Here it feeds during the late fall, winter and early spring when hydric vegetation is unavailable. Its favorite foods at this time are the tops of paper birch, aspen, striped maple, moosewood, dwarf maple, twigs of balsam fir, mountain ash, herbaceous growths like the everlasting pea and numerous shrubs and other small deciduous trees. The climax stands have throughout a sparse growth of this type of vegetation which is found more abundantly in the subclimax. In general the shrub and herbaceous vegetation of the subclimax occurs sparingly in the climax. The center of any climax stand has necessarily a sparse ground cover but as the edge of the climax is approached it becomes more luxuriant and abundant. This will explain the occasional occurrence of moose and other large herbivores in the climax itself. The broken, discontinuous nature of climaxes, and the general distribution through them of distinctly subclimax areas makes it possible for certain large ungulates to actually live within the climax itself.

The caribou (table I) is represented by four or five species and varieties, but only a part of them appear to have any significance from the standpoint of habitat relations in the coniferous forest (fig. 6). The variety *R. caribou* reaches from the Atlantic Coast to the Rocky mountains. *R. sylvestris*, which is an equivalent, has been recorded from the west coast of Hudson Bay to the east shore of Great Slave Lake (Harper, '32). Kermode ('09) states that *R. mcquirei* occurs north of British Columbia in Alaska. Clarke ('12) indicates that *R. osborni* occurs from northern British Columbia to about 54°. Kermode ('09) and Osgood ('09) indicate that *R. montanus* occurs throughout the British Columbia while its southward extension into the United States is well known.

[9] Climax as used here is relative and it is still a moot question as to whether or not jack pine, black spruce, even aspen and birch may not in limited areas be climax as well as subclimax. They often are mixed with trees of the generally accepted climax.
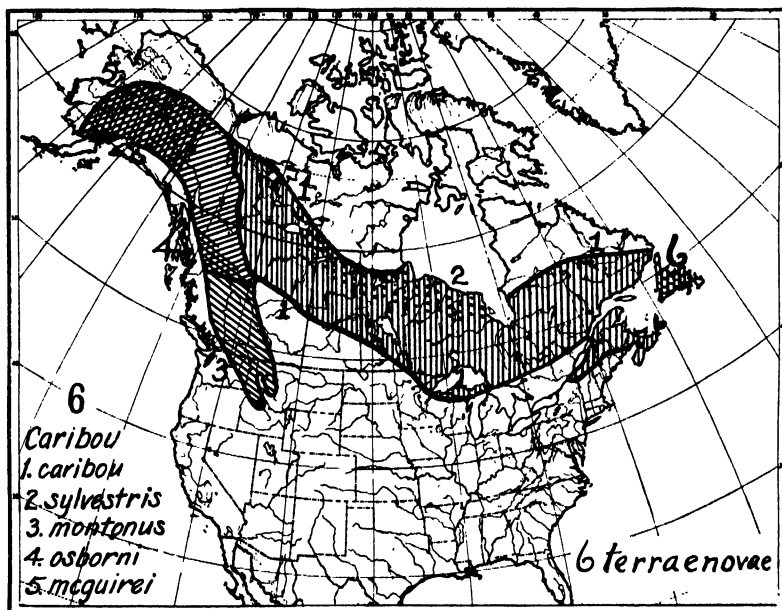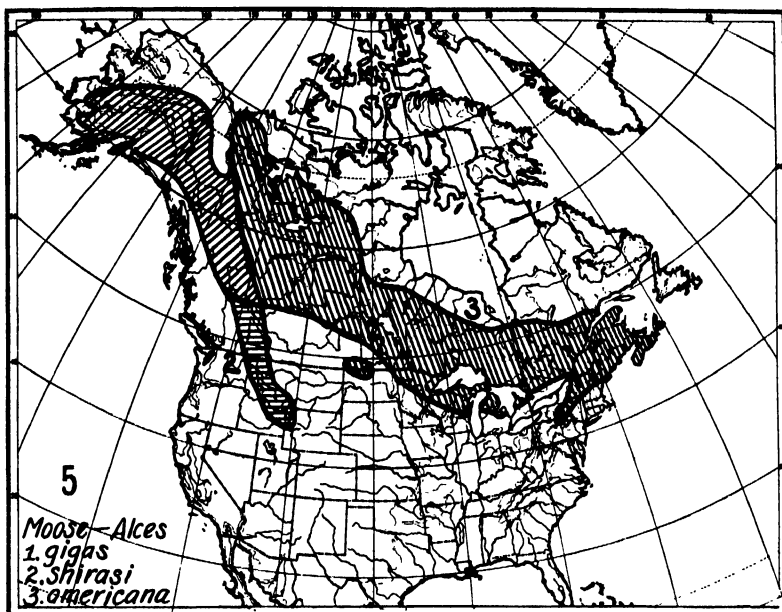
FIG. 5. The distribution of the moose (*Alces*); *A. gigas* is a distinct species while the other two are subspecies of *A. americanus, A. a. americanus* and *A. a. shirasi*.

FIG. 6. The distribution of the woodland and mountain caribou, species and subspecies. The ranges of *R. montanus, R. osborni,* and *R. macquirei* overlap and the limits are not well known. The *R. sylvestris* area is indicated; one Newfoundland species is ecologically equivalent to *R. caribcu*.

The principal food of these species resembles closely that of the moose with the exception that they depend on the mosses and lichens in addition to browse, and only occasionally feed on aquatic and subaquatic vegetation.
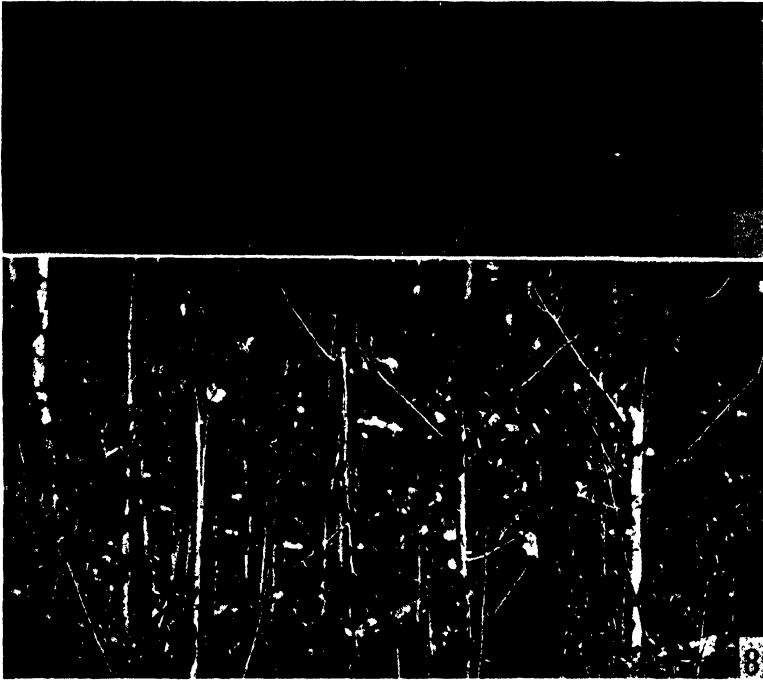


FIG. 7.   The summer brouse of the moose—yellow water lily with leaves blossoms eaten off; the caribou takes the same food at times.

FIG. 8.   The winter brouse of the moose—aspens cut off at the top.

Browse includes such climax and subclimax shrubs and trees as paper birch, aspen, striped and mountain maple, cherry, serviceberry, hazel, moosewood, blueberry, bearberry, and crowberry which are largely xeric, and alder, willow, dwarf birch, dogwood, blueberry and leather-leaf, which are hydric.   During the summer they feed on mosses and lichens of the climax and subclimax such as the *Cladonia* spp., *Cetraria* spp., and *Sterocaulon paschale*.   Grasses and various herbaceous plants mostly hydric, form an important part of their diet during this period.  · During the winter, however, when many of these forms are so deeply covered with snow that they cannot be reached, they are forced to feed upon tree growing types such as the common   *Usnea barbata*, old man's beard, which hangs from the lower branches of black spruce and larch, and on *Sticta pulmonaria*. ` If the caribou were to be judged by its moss and lichen eating proclivities alone, it would be classified as a climax or late subclimax animal, but the fact that it is also a browser shows its dependence upon the subclimax as well.

The gray wolf is represented by four species (table I). The timber wolf feeds largely upon the varying hare, moose, caribou and deer, as well as upon all forms of wild life which come its way. Although it ranges widely over both climax and subclimax in pursuit of food, the bulk of its food supply is found necessarily in the subclimax. Contrary to accepted opinion, the wolves, except during short periods, feed largely upon the smaller forms of life and do not attack the larger ungulates unless forced by the failure of their normal food supply.

The black bears are found throughout the transcontinental forest (fig 3) either as the American black bear or its equivalent species. It is omnivorous, eating anything that grows, from fruit, roots and vegetation of many types to insects, fish and mammals. It ranges over both climax and seral stages, but prefers the subclimax inasmuch as in such areas a variety of plant and animal food is present. It feeds in season upon practically all the berries and fruits listed (p. 380). Most of these are found sparsely scattered through the climax stands and along its edges but never in abundance except in the subclimax. They were less abundant in coniferous than in deciduous forest. In 1822 David Crockett killed 105 bears on not more than 30 or 40 square miles in West Tennessee. Bears were scarce along the wooded streams of the great plains and in the badlands (Bailey, '26) (fig. 3).

Jackson ('26) records the midcontinent grizzly as far east as The Pas, Manitoba. The Alaska grizzly occupies the spruce-pine association. There is a striking similarity in the food of all bears in the coniferous forest. During hibernation, the bear often seeks the protection and shelter of the denser climax stands.

The wolverine also ranges throughout the subordinate communities of the biome as well as through the climax, confining its activities to the ground and feeding on all forms of animal life and only occasionally on berries. Even though it is comparatively small, it has been known to kill deer, caribou, and even moose. For the bulk of its food, however, it depends upon the smaller herbivores, such as the rabbits, ground squirrels, mice, voles, etc. Like the bear, it will eat anything which comes its way in the form of animal life, carrion or otherwise, and often robs trappers' food-caches and bait when other food is scarce.

The lynx is represented by three species (table I, fig. 11). While the statement is made that the lynx ranges from the Atlantic to the Pacific, they occur only on the east slope of the Cascades in Washington (Taylor and Shaw, '29) and Oregon, and are wanting on Vancouver Island. No records were found for the coast of the mainland of British Columbia. It is primarily a creature of the deep coniferous forests and like the marten retreats before the advance of the lumberman. It is unlike the bobcat in this respect, which prefers the broken, partly open country. In food habits, however, the two are the same, both living largely upon hares and rabbits, varying this diet with small rodents and birds.
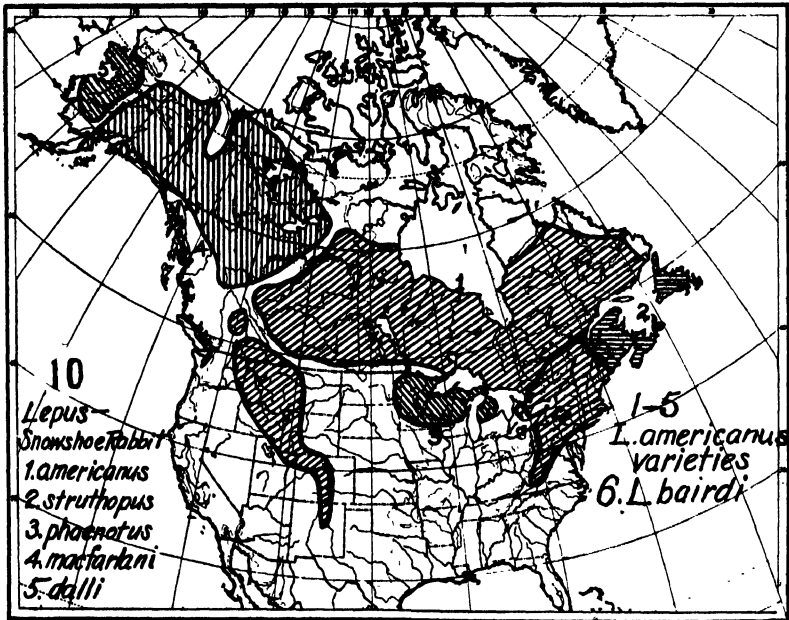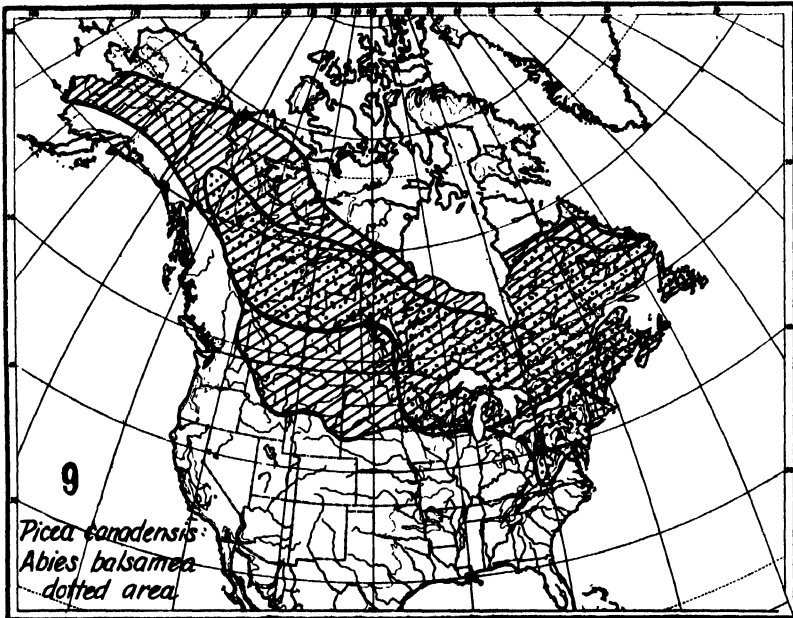
FIG. 9.  The distribution of two climax trees.  (*P. canadensis* = *P. glauca* of text.)

FIG. 10.  The distribution of the snowshoe rabbit.  Compare with figure 1 for agreement and disagreement between subspecies and associations.
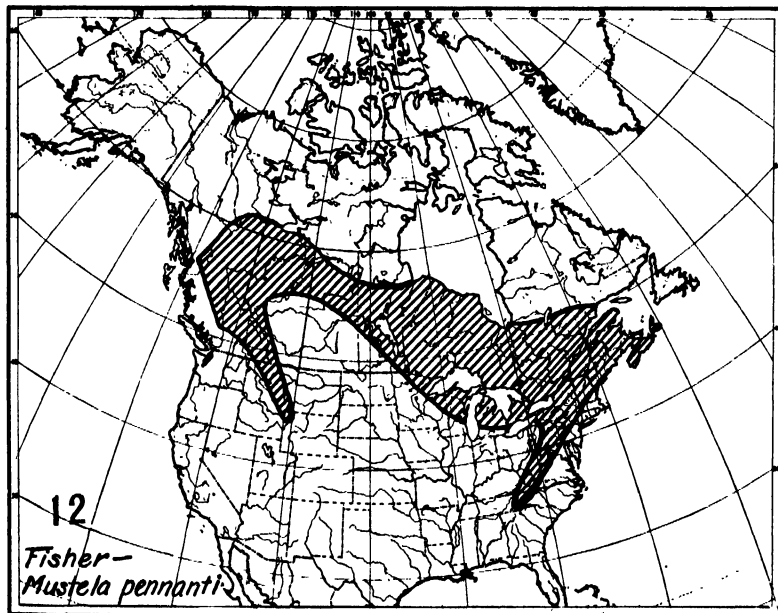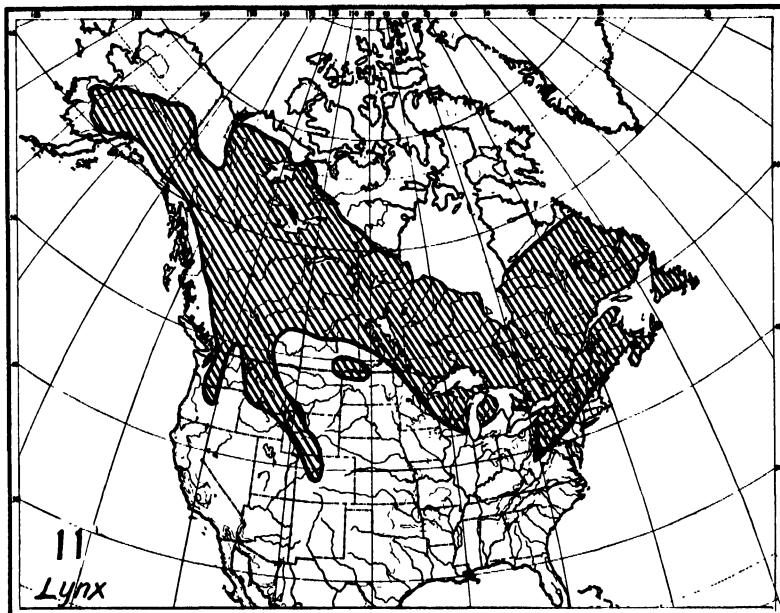
FIG. 11.  The distribution of the lynx (*Lynx canadensis*); it covers all three transcontinental associations and extends southward into the mountain forest.  *L. subsalonus* (Newfoundland) and *L. c. mallipilosus* (Alaska) appear to be mixed with *L. canadensis*.

FIG. 12.  The distribution of the fisher, *Martes pennanti* of the text,—the single Pacific coast subspecies is not indicated.

Due to its inherently shy and nocturnal nature and its need for shelter and hiding, the lynx is most often found in the deep forest shade of the old climax stands.   Inasmuch as it depends for its food supply upon the varying hare, it is self-evident that it must do the bulk of its hunting in the swales of alder, willow, and black spruce where this animal is most abundant.   The very fact that snares for lynx are always set in rabbit runways in such locations verifies this assertion.   It can be said then that though the lynx may live and die in the climax, it depends upon the subclimax for its food.

### B.   Minor Permeant Influents

In addition to the major influents, there are the minor permeant influents with similar habits, which exact a lesser toll from the vegetation and are in turn preyed upon by the large and the small carnivores.

The porcupine takes heavy toll of the deciduous trees such as birch, alder, and poplar.   These records appear to much outweigh those of damage to conifers in the forest under discussion.   This may be due to lack of herbaceous food in the very close stands of deciduous trees.

The varying hare is represented by several species as shown by table II (fig. 10).   It feeds upon vegetation found largely in the subclimax areas and is seldom found in any number in the climax except where it is broken permitting subclimax deciduous plants to grow.   Grange ('32) states that the Minnesota varying hare never reaches abundance in climax hardwood areas.   Of the subclimax areas it prefers the hydrosere and is found most abundantly in bog margins where the alder, willow and sedges grow most luxuriantly.   It is also found in the xerosere, but only where there is a thick stand of aspen and birch.   The ideal location is a swamp bordered with alder and willow, surrounded in turn by a grove of aspen or birch or both. Pure climax stands are practically devoid of a rabbit population.   The following are food plants of these species: Aspen, birch, alder, willow, sedges, grasses, all herbaceous growths. buds and shoots of deciduous plants. Only the bark and tips of the larger shrubs and trees mentioned are eaten and this type of food is utilized only when all smaller and more succulent types are unavailable.   The varying hare has a well known effect on the woody vegetation through the eating of bark in winter (Bird, '30, Grange, '32), which results in the girdling of young trees.   They are especially fond of aspen which suffers often.   Variation in abundance of the hare makes its effect rhythmic rather than constant, otherwise it might be classed as a major influent.

In the case of the other herbivores, although the effect upon the vegetation is not as noticeable as in the case of the major permeant influents, still collectively they are an important factor.   This also holds true for the smaller carnivores which affect directly through competition, the food supply of the larger forms.   The killing of rabbits, for instance, by owls, weasels, and hawks, may result in an increased toll of moose, deer and caribou being

taken by wolves and a consequent lessening of the reaction of those particular forms on their respective habitats.    The minor influents are more variable in numbers and intensity of coaction than the major influents.

TABLE II.    *Minor permeant influents of the different associations.**

|  | Des. | SB | PH | SP |
|---|---|---|---|---|
| *Erethizon dorsatum dorsatum* (Linn.), porcupine | 19 | x | x |  |
| *Erethizon epixanthum myops* Mer., porcupine | 20 |  |  | x |
| *Lepus americanus americanus* Erx., varying hare | 21 | p | p |  |
| *Lepus americanus macfarlani* Mer., Mackenzie varying hare | 22 | p |  | x |
| *Lepus americanus struthopus* Bangs, Nova Scotia varying hare | 23 | p |  |  |
| *Lepus americanus phaeonotus* All., Minnesota varying hare | 24 |  | p |  |
| *Lepus americanus dalli* Mer., Dall hare | 25 |  |  | x |
| *Martes pennanti pennanti* (Erx.), fisher (Fig. 12) | 26 | x | x |  |
| *Perisoreus canadensis canadensis*, Canada jay | 27 | x | x |  |
| *Perisoreus canadensis fumifrons*, Alaskan jay | 28 |  |  | x |
| *Penthestes hudsonicus hudsonicus*, Hudsonian chicadee | 29 | p | x | x |
| *Evotomys gapperi gapperi* (Vigors), red-backed vole | 30 | x | x |  |
| *Buteo lagopus s.johannis*, American rough legged hawk | 31 | x | x | x |
| *Bonasa umbelloides*, gray ruffed grouse | 32 | x | x | x |
| *Mustela vison vison* Sch., mink 46, 21, 24, 23, 61 | 33 | x | x |  |
| *Dryobates villosus septentrionalis*, hairy woodpecker | 34 | p | x | x |
| *Mustela rixosa rixosa* (Bangs), least weasel | 35 | p | x |  |
| *Mustela cicognanii cicognanii* Bon., Bonaparte weasel | 36 | x | x | x |
| *Marmota monax canadensis* (Erx.), woodchuck | 37 | x | x | x |
| *Colaptes auratus luteus*, northern flicker | 38 | x | x | x |
| *Canachites canadensis canace*, Alaska spruce grouse | 39 | p |  | x |
| *Canachites canadensis osgoodi*, spruce grouse | 40 | x | x |  |
| *Haliaeetus leucocephalus alascanus*, Alaska bald eagle | 41 | x | x | x |
| *Ixoreus naevius merulcides*, northern varied thrush | 42 |  |  | x |
| *Ceophloeus pileatus picinus*, western pileated woodpecker | 43 |  |  | x |
| *Microtus drummondii* (A & B), Drummond vole | 44 | x | x | x |
| *Ondatra zibethica spatulata* (Osg.), muskrat 24 | 46 | x | x | x |
| *Ondatra zibethica alba* (Sabine), muskrat | 47 | p |  |  |
| *Lutra canadensis canadensis* (Sch.), otter | 48 | x | x | x |

* For meaning of letters and figures in columns see footnote, table I.

The jays, woodpeckers, chickadees, in addition to the other insectivorous types enumerated in the tables, exert a certain amount of influence on the habitat by feeding on insect pests which otherwise might become numerous enough to affect vegetation seriously.    There is no question but that the woodpeckers play an important part in controlling the larch sawfly, and such bark and bud feeders as the chickadees, nuthatches, and others take toll of insect forms such as the spruce budworm, various scale insects, beetles, and larvae.

The weasel, fisher, and mink exert an important influence in that they compete with the larger carnivores to a certain extent for the small rodentia which form in the northern coniferous forest, the bulk of the food of all flesh eating animals.    Under this classification may also be mentioned the birds of prey such as the owls, hawks, and eagles.

The muskrat is of particular importance in that it feeds to a certain extent on the food of the moose and occupies exclusively what becomes the

summer feeding ground for this ungulate, the shores of lakes and rivers well grown with aquatic vegetation such as the waterlilies. A thriving rat colony will quickly ruin a feeding ground for moose and cause them to move elsewhere. The beaver likewise is important in maintaining extensive aquatic areas for the moose and muskrat while competing to some extent with other bark eaters.

## C. Subclimax Arthropod Influents

Because of their blood sucking propensities, certain arthropods often have a great indirect influence on vegetation. The moose as well as the deer and caribou during fly seasons are forced to spend much time in the water, and choose waters with a rich growth of edible plants. The phytophagous species could perhaps be evaluated by comparison with work of major influents. Many of these are characteristic of seral stages some early and some later. Budworms, bark beetles, and sawflies (table III) do a striking amount of damage when abundant.

TABLE III. *Subclimax and other seral influents and subinfluents* *

| Influents | Des. | SB | PH | SP | Range | |
|---|---|---|---|---|---|---|
| | | | | | FP | WD |
| *Peronea variana* Fern, black-headed budworm FP; fir, balsam, spruce, hemlock, larch................... | 49 | x | x | x | | |
| *Bucculatrix canadensisella* Chambers, birch leaf skeletonizer FP; birch................................ | 50 | x | x | x | x | |
| *Polygraphus rufipennis* Hartig, four-eyed bark-beetle FP; spruce, black spruce and larch................... | 51 | x | | x | x | |
| *Lygaeonematus erichsoni* Hartig, larch sawfly FP; larch.. | 52 | x | x | | x | |
| *Neodiprion* sp., jack pine sawfly FP; jack pine........ | 53 | x | x | | | |

| Subinfluents | | | | | | |
|---|---|---|---|---|---|---|
| *Agriotes limosus* Lec., click beetle.................... | 54 | x | x | | | |
| *Nabis rufusculis* Reut., blueberry nabid (predatory).. .. | 55 | x | x | | | x |
| *Tetrognatha extensa* L., long-bodied spider............. | 56 | x | x | x | | x |
| *Rana septentrionalis* Baird, frog..................... | 57 | p | x | | | |
| *Rana cantabrigensis* Baird, frog..................... | 58 | p | x | x | | |
| *Pseudacris nigrita septentrionalis* (Boul.), spring peeper.. | 57a | x | x | | | |

* The food plants of the insects are indicated following FP in connection with the common names in column one. For the meaning of columns see footnote, table I. In columns under Range, x in the FP column indicates that the species occurs in scattered food plants outside the biome; x in the WD column indicates a wide range outside the biome not related to particular plants.

Various small coldblooded vertebrates and arthropods also are present but exercise a very minor influence in the community.

### D.   Climax Influents

There are several species which range through much of the biome climax and are more or less limited in their range by the extent of the climax growth.   In potency of effects, they rank with the wide ranging influents discussed in the preceding section.

TABLE IV.   *Climax minor influents* *

|  | Des. | SB | PH | SP |
|---|---|---|---|---|
| *Martes americana americana* (Tur.), American marten . . . . . . . . . . | 59 | p | x | |
| *Martes americana abieticola* Preble, Hudson Bay marten . . . . . . . . . | | p | | |
| *Martes americana actuosa* (Osg.), Alaska marten . . . . . . . . . . . . . | 60 | | | x |
| *Sciurus hudsonicus hudsonicus* (Erx.), red squirrel . . . . . . . . . . . . . | 61 | x | x | x |
| *Glaucomys sabrinus sabrinus* (Shaw), flying squirrel . . . . . . . . . . . . | 62 | x | x | |
| *Glaucomys sabrinus yukonensis* (Osg.), flying squirrel . . . . . . . . . . . | 63 | | | x |
| *Canachites canadensis osgoodi*, Alaska spruce grouse . . . . . . . . . . . . | 64 | p | | p |
| *Canachites canadensis canace*, Canada spruce grouse . . . . . . . . . . . . | 65 | p | x | |

* Columns as in table I.

The squirrels exert their greatest influence not through their feeding but through their habit of storage in which they bury great quantities of cones of pine and spruce as well as the fruits of hazel and rose (*Rosa acicularis*), cherries, plums, etc., many of them germinating the following season.   The bulk of the food of the squirrel is the seed of the spruce and pine so it is dependent primarily upon climax stands.   The fruits of climax subdominants which occur sparsely throughout the climax or along its edges are also utilized but are of no great importance.

The marten never ranges outside of the climax coniferous forests, feeding largely upon the smaller herbivores such as squirrels, mice and voles.   However, it will not disdain insects, grubs, small reptiles, carrion or even the berries of the mountain ash.   It is arboreal in habit and is seldom if ever found in anything but the very densest stands of timber and invariably migrates with the cutting or burning of this type of vegetation.

The spruce grouse or fool-hen during the winter months feeds upon the buds and tips of spruce and pine.   The porcupine exerts considerable influence upon both pine and spruce due to the girdling of young trees.

### E.   Climax and late Subclimax Arthropod Influents

The Anthropod influents include several bark beetles and bud worms attacking several of the coniferous trees.   These are confined to no single tree and few or none to a single association (table V).

### IV.   THE BIOTIC COMMUNITY AND THE DISTRIBUTION OF SPECIES

The idea that a biotic community is an assemblage of organisms of which a combination of abundant individuals of certain species is charac-

teristic, has received too little recognition. It must be noted further that there are definite interrelations among the individuals of the species abundantly represented as well as among individuals of all other species in the community. The community concept is fundamentally quantitative and social, in other words, based upon abundance and interdependence or upon population and interactivity.

TABLE V. *Climax insect influents* *

| | Des. | SB | PH | SP | Range | |
| | | | | | FP | WD |
|---|---|---|---|---|---|---|
| *Ellopia fiscellaria* Guen., hemlock looper (balsam fir, hemlock) | 66 | x | x | | | |
| *Cacoecia fumiferana* Clem., spruce budworm (balsam fir, red spruce) | 67 | x | | | | |
| *Dendroctonus piceaperda* Hopk., eastern spruce bark beetle (white and black spruce, white and red pine) | 68 | p | x | | x | |
| *Dendroctonus borealis* Hopk., spruce bark beetle (white spruce, Englemann spruce) | 69 | p | | x | | |
| *Pilyoktemes sparsus* Lec., balsam fir bark beetle (balsam fir) | 70 | x | | | x | |
| *Dendroctonus rufipennis* Kirby, white pine bark beetle (white pine and jack pine) | 71 | x | x | x | | |
| *Calicella impatieus* (Walk), mosquito | 72 | x | x | x | | |

* Columns as in table III. Names of food plants follow the common names of insects in parentheses.

Maps of the distribution of plants and animals are not even quasiquantitative. They are often made from records in literature or from museum specimens. The area roughly indicated by dots representing actual records, many of which are dependent upon very local conditions, is enclosed and used as representing the area covered by the plant and animal species in question. The maps of the distribution of a particular species do not necessarily agree with the distribution of the community in which individuals belonging to the species play an important role.

The set of maps (figs. 1–6, 9–12) are designed to show this principle and the necessity for interpreting them with regard to communities, abundance, and uniformity of distribution. The white pine (fig. 2) is an example. This tree was a dominant over extensive areas about the Great Lakes, but in Iowa, Illinois, Indiana, Ohio, and the southern portions of Minnesota, Wisconsin, Michigan, and the lowlands of the eastern states only occasional small groves and single trees occurred. Even the varying hare or snowshoe rabbit (fig. 10) has a more restricted range. It, however, is a subclimax animal, and as it has already been stated, never becomes abundant in climax deciduous areas. The fisher and marten, however, do not extend outside the range of considerable areas of continuous coniferous forest (fig. 12) and

have a distinct preference for the climax.   The marten extends only a little farther south than the fisher.   The white pine as a climax tree, extends farther to the southeast than either the subclimax rabbit and the climax marten and the fisher.   There are no data on the continuity of the populations of these animals.   Recourse can only be had to the details of the habits and habitat preferences.   In the case of the marten, the annual cycle of relations, and in the local range of the individual, the breeding relations, including the hiding places for the young, are confined essentially to the climax stands of coniferous trees.   In areas where there is a deciduous climax it is not reasonable to suppose that they were any more abundant proportionally than are the areas of coniferous woodland.

The moose presents as close adherence to the coniferous forest as could be expected of any animal of the climax.   The black bear is distinguished by being in two or more biomes but is less widely ranging than some plants, see figure 3.   The geographical range of animals appears closely tied up with the habitat relations.   Suitable breeding places are very important in determining the presence and abundance of the individuals of any species. Inasmuch as they are usually located in close proximity to food, the breeding places in themselves become important indicators, and their abundance is a limiting factor for both presence and abundance.

## V. Comparison of the Three Associations of the Biome

Of the three biotic associations which are embraced within the boundaries of the biome, it is of note that two, the pine-hemlock, spruce-balsam fir, in which the climax dominant plants are so radically different (pine and hemlock opposed to balsam spruce and fir) resemble each other closely by having a great number of identical or equivalent animal forms ranging through them.   The climax influents common to both associations are: red squirrel, flying squirrel, marten, spruce grouse, red backed vole, and porcupine. Major influents and influents of wide range in these associations are species or subspecies of the moose, caribou, wolf, lynx, otter, wolverine, rabbit, fisher, Canada jay, yellow warbler, chickadee, horned owl, northern flicker, hairy woodpecker, weasel, Canada woodchuck, bald eagle, rough-legged hawk, ruffed grouse, mink, and muskrat.   The *Pinus-Picea* association of the Yukon and the Northwest although it possesses equivalent types of practically all of the influents mentioned, has, probably, at least four mammals, the wolverine, red squirrel, least weasel, and otter, which are found as the same subspecies in the other associations.

The influents of the *Pinus-Tsuga* and *Picea-Abies* associations are limited to geographical varieties of wide ranging species more properly considered as subspecies without habitat differentiation than as poorly differentiated equivalent races.   In this case, the woodchuck (*Marmota monax canadensis*) is one of the few species showing even variable differentiations.   Also the flying squirrel (*Glaucomys sabrinus*) may be characterized more accurately as

a subinfluent than as an influent.    Outside of the permanent residents in the above climaxes such as the horned owl, Canada jay, Hudsonian chickadee, and hairy woodpecker, there are comparatively few birds found there even during the breeding season.    Among the more common are the eastern ruby-crowned kinglet, *Corthylio calendula calendula*, Canada warbler, *Wilsonia canadensis*, cross-bills, *Loxia curvirostra pusilla*, *L. curvirostra percna*, *L. leucoptera*, yellow warbler, *Dendroica aestiva aestiva*, and red-eyed vireo, *Vireo olivaceus*.    In general it might be said that the climaxes are characterized by comparatively few mammals and birds except where they come in contact with subclimax vegetation.

Major permeant influents of the *Picea-Pinus* association of the northwest are the Alaska moose, Alaska grizzly bear, wolverine, Alaska yellow porcupine, Osborn's and McQuire's caribou, the northern grey wolf, arctic lynx, Yukon flying squirrel, Alaska red fox, Alaska marten, least weasel, Alaska mink, otter, Yukon ground squirrel.    Among the birds may be mentioned the following: Alaska spruce grouse, Alaska bald eagle, northern varied thrush, western pileated woodpecker, Canada jay, northwestern horned owl. In this case the white spruce is an important binding dominant along with red squirrel, the weasel, etc. as binding influents.

## VI. Discussion

The preceding pages serve to bring out the close dependence of the major influent and other biotically potent animals upon the area occupied by the coniferous forest biome which is indicated by plant climaxes.    The plant climax is accepted as the guiding principle in the evaluation of the subclimax stages and as delimiting the biome.    The writers know no better law of nature which may be used in the interpretation and description of natural land communities.    Without community development (succession) and the climax the natural communities would have remained in chaos.    The knowledge of fluctuation and migration is very important in developing the climax idea.    The relations of animals to the vegetation is such that without the use of the laws of community development, habitat relations would be difficult of description and interpretation.    This is not an attempt to lessen the importance of a thorough understanding of fluctuations, migrations, succession and climax in the interpretation of communities or of the plant climax with its animals as an indicator of climate.    The facts brought out indicate the agreement of the limits of climaxes and of animal influents, even though the latter, in some cases, are dependent primarily upon the subclimax stages of the biome.    It must be kept in mind that the climax is the great delimiting factor (for the subclimaxes) and though an animal may be inherently a subclimax type, it nevertheless is directly dependent for the range boundaries upon the extent of the climax itself due to its dependence on climate.

Furthermore it has been brought out that plants have geographical

ranges greater than their dominant area and animals outrange their area of important influence (figs. 2, 4, and 9).

The data show the importance of considering animals in setting up biotic units.    They indicate weaknesses in the idea of biomes built on plant data alone.    It has been noted in the case of the pine-hemlock community that in its subclimax stages and in its major and minor permeant influents and influents of lesser ranks and even unimportant animal species, it has a clear unity with the transcontinental spruce-balsam fir association and even with the Alaskan spruce-pine association.    The pine-hemlock community is therefore not to be interpreted as a distinct biome, but rather as an association of the coniferous forest.

Besides the rather distinct differences between the climax pine-hemlock community and the other two climaxes, there are several examples of similar relations.    The beech-maple association has all of the essential characteristics of the pine-hemlock association.    Its unity with the biome being based upon the developmental stages and subdominant plants, but is perhaps not segregated into as definite an area.

The coniferous forest climaxes of the Rocky mountains and Sierras have not been fully analyzed as yet.    The evidence in hand indicates that they are not of formational rank but represent associations, perhaps one or more montane, and one or more subalpine associations.    (See Rasmussen '36 in press.)    The latter doubtless extends northward for some distance above the spruce-pine association.

The evidence suggests the necessity in certain cases for setting up even larger units in bioecology than are commonly recognized by the American and English plant ecologist.    The results of more comprehensive study of vegetation alone (without animals) has usually tended toward the recognition of larger units than were first identified.    Clements ('20, p. 115) writing on the grassland, indicates this tendency.    "Pound and Clements (1898: 243, 1900: 347) recognized two prairie formations. . . . However the developmental concept of the formation had broadened its scope and afforded a clearer view of its structure.    As a consequence of a special study of these relations it became necessary to abandon the view of two separate grassland formations, and to recognize a single formation composed of several associations."    Again Du Rietz ('30) shows a table in which he has moved his term "association" so as to cover a community two degrees larger on his scale, as expressing the differences between his 1927 and 1930 views.    Items in his table suggest that other plant ecologists (e.g. Drude) have made similar changes.

There is considerable discussion and dispute between those who emphasize large units and those who emphasize small ones, as suggested by Du Rietz in 1930.    Certain plant ecologists working on the continent of Europe, appear to be dealing with the minute details of all sorts of aggregations and variations of arrangement of dominants or even of plants of secondary or

tertiary importance such as forest herbage. As animal ecologists, it is difficult for the writers to find parallels in the distribution of land animals, however, there appears to be a parallel to the details of plant distribution in the arrangement of animals (chiefly mollusca, barnacles) in the tidal communities. Barnacles usually belonging to two or three species are found in any area between the tide lines. They are the most important dominants. The density and arrangement of these varies from point to point. Some species drop out, some occur alone; there are combinations of two or three species with or without mollusca such as *Mytilus* and again all are found together. The detailed study and mapping of the arrangement of these species is not an important matter. The reason for this fact is indicated in the work of Rice ('35) on barnacles. This writer shows that a complicated chain of almost accidental weather events may lead to a particular arrangement. A slightly different series of meteorological conditions is capable, in the next life cycle, of giving an altogether different local arrangement of either plants or sessile animals in the same area. Since the series of events giving the arrangement cannot be reconstructed the arrangement cannot be given significance.

The factors controlling the pattern of the various aggregations are important, but are ascertainable only either by experimentation or by a detailed knowledge of the original location of all disseminules followed by close observation of the fate of each. The conditions for the second type of determination are difficult or impossible of attainment, especially in the case of plants. This puts these details of aggregation arrangement into the field of experimentation. The chief motive for observation is to ascertain the role of competition.

Physical factors also play a role with large animals. The great variation in the extremely widely distributed foods of such animals as the moose, would lead the animal over a much wider area if food was the factor controlling its distribution. Furthermore, such a large variety of plants in the dietary leads to the conclusion that many other plants might easily be substituted if their utilization became essential.

The use of the climax and seral stages in designating the habitat relations of influents is important. It places their relations in terms which can be seen and understood in the field. The permeant influents due to their preference for the subclimax stages leave profound effects upon succession which have been all too little studied, due to the fact that plant ecologists have rarely taken animals into consideration.

Plant ecologists usually regard dominance as a result of reaction on the habitat. Another type of dominance not generally recognized is strongly suggested if not actually demonstrated in the sea (Peterson, '18, p. 16–18). It results from actual effect on the community constituents. A potent coactor may entirely eliminate certain community constituents while others due to some superiority are able to remain abundant while receiving impact

of the coactor which thus produces a community of peculiar composition in which it is a dominant (Shelford, '31; p. 464). This type of dominance can be determined only through long continuous observation probably accompanied by extensive enclosure and exclosure experiments.

The extensive modification of vegetation cover, destruction of certain carnivores, and agricultural operations, have greatly changed the environments available to animals. They often have taken up haunts under the modified conditions which analyses show to be essentially the subclimax habitats normally preferred. Even though one recognizes a highly regulatory character for animal habits (Elton, '30), he does not often have to appeal to changes in habits in explaining distribution, especially distribution as changed by settlement. Abundance of the individuals of the species concerned were not generally noted in the early species-describing period of natural history. Mere presence of scattered individuals is usually not important ecologically, but presence in numbers sufficient to have an effect on a community is significant. All maps of distribution must be analyzed from both the standpoint of life habits and abundance.

The question naturally arises as to the disposal to be made of migratory species. Generally speaking, these are frequently seasonal influents classed in seasonal communities in two biomes. The coactions and reactions must be evaluated in each community affected. It is further probable that the more migratory small birds would not be ranged as major or even minor influents even if present throughout the year. The large aquatic birds rarely have a seasonal influence extending beyond the earliest seral stages.

## VII. Summary

1. Most of the large ungulates and corresponding flesh eaters of the coniferous forest biome range over the climax and subclimax stages and often have a preference for the subclimax plant communities, though most of them are restricted to the area of the biome climaxes. The influent species and races exceed the limits of their biomes with a frequency about equal to that of the climax dominant plants. A few animals are restricted to climax conditions.

2. Numerous animals are characteristic of early seral stages and when restricted to them are often widely distributed.

3. The primary unit of bioecology is the biome, a community of formational rank in the largest sense of the term. The biome is characterized by uniformity of physiognomy of the plant climaxes and in a lesser way by the subclimax stages. It is characterized by a combination of major and minor permeant influent animals, a few climax influents, and many small influents and subinfluents. A certain grouping of species and varieties is characteristic of each biome.

4. The biotic association is a subdivision of the biome. · It is a climax community with uniformity of plant physiognomy and a taxonomic compo-

sition of greater refinement as regards both plants and animals, than characterizes the biome as a whole. It contains characteristic community constituents, either plant or animal. The plant characteristics of two associations may be strikingly different, while the important animal influents are the same, *i.e.*, characteristic of both. In such a case the difference between the two is greatest as regards plants; in another case the difference may be greatest as regards animals. The two types of associational differentiation are illustrated by the North American transcontinental forest as follows:

*a.* Plant climax distinct from the rest of the biome as to taxonomic composition; characteristic influent birds and mammals and insects few or wanting; important influents and subclimax stages similar to the adjacent parts of the biome; example, pine-hemlock association in the region of the Great Lakes.

*b.* Climax sharing a part of its plant dominant species with the other associations; a considerable number of species or races of major influent animals distinctive in the area of the particular association. Some climax influents characteristic; example the pine-spruce association of northwestern Canada and Alaska.

5. Animal dominance due to effects on the community probably exists on land as well as in the sea.

## VIII. Acknowledgments and Bibliography

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# THE HEMLOCK – WHITE PINE – NORTHERN HARDWOOD REGION OF EASTERN NORTH AMERICA[1]

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## INTRODUCTORY

Sargent, in his report on the forests of North America (1884), distinguishes the "northern pine belt" (fig. 1) as one of six natural forest divisions
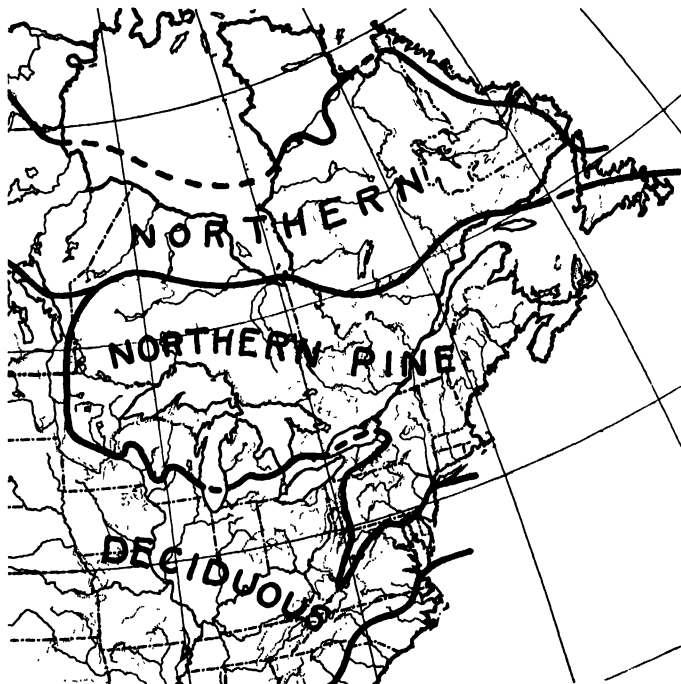


FIG. 1. Map showing the "northern pine belt," as delimited from the adjoining northern forest and deciduous forest regions by Sargent (1884).

of eastern North America, a procedure in which he is followed by Schimper ('03). "This division of the Atlantic forest," writes Sargent, "may be characterized by the white pine, *Pinus strobus*, its most important if not its most generally-distributed species." It is this region, somewhat more narrowly circumscribed, which furnishes the subject of the present paper; more especially, it is the question of how the climax forests of this region

should be regarded, from an ecological point of view, in relation to those which characterize the country farther north and farther south respectively. The region under consideration is coextensive or practically so with the "northern hardwood" region of Frothingham ('15; fig. 2), with the north-
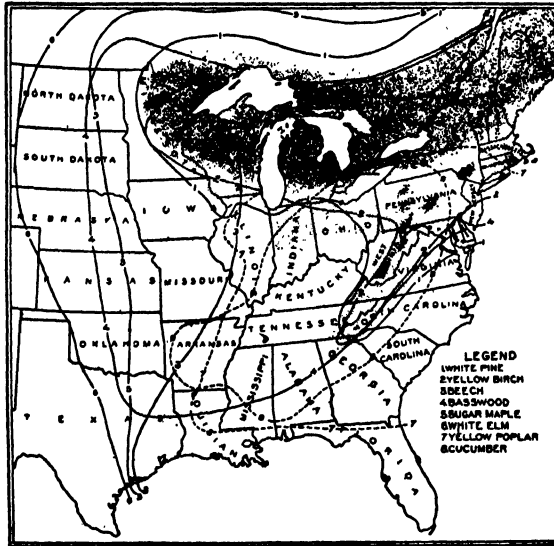


FIG. 2.  Map showing the "northern hardwood" region, as delimited by relative abundance of northern hardwoods in the forest.   (After Frothingham '15.)

eastern "transition forest" region of Nichols ('18), and with the "Great Lake" or "south Canadian forest" region of Hardy ('20). It corresponds roughly with the "St. Lawrence–Great Lake" region of Harshberger ('11) and the "lake forest" region of Weaver and Clements, '29 (fig. 3), although somewhat more far-reaching than either.   In terms of its more character- istic climax constituents, the area may appropriately be designated the "eastern hemlock–white pine–northern hardwood region"; for purposes of convenience, it may be referred to simply as the "eastern hemlock region."

The approximate geographical extent of the eastern hemlock region, as interpreted by the writer, is shown on the map (fig. 4).   Centering around the Great Lakes and the St. Lawrence basin, it is flanked along its northern borders by the vast region of northern coniferous forest, or "taiga," which extends from east to west in a wide belt from the Labrador peninsula to Alaska.   Toward the south it impinges on the region of deciduous forest which occupies much of the eastern United States, having its center of development in the southern Appalachian Mountains and the Ohio basin. In terms of the climatic climax, the vegetation of these two neighboring regions may be characterized briefly as follows.   The northern conifer for- est, monotonously uniform over vast stretches of country, is impressive in
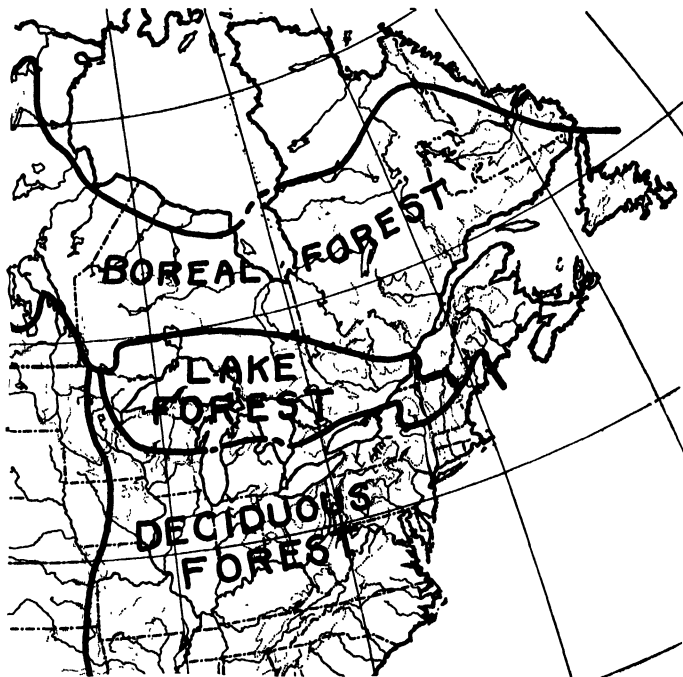
FIG. 3.   Map showing the "lake forest" region, as delimited by Weaver and Clements ('29)
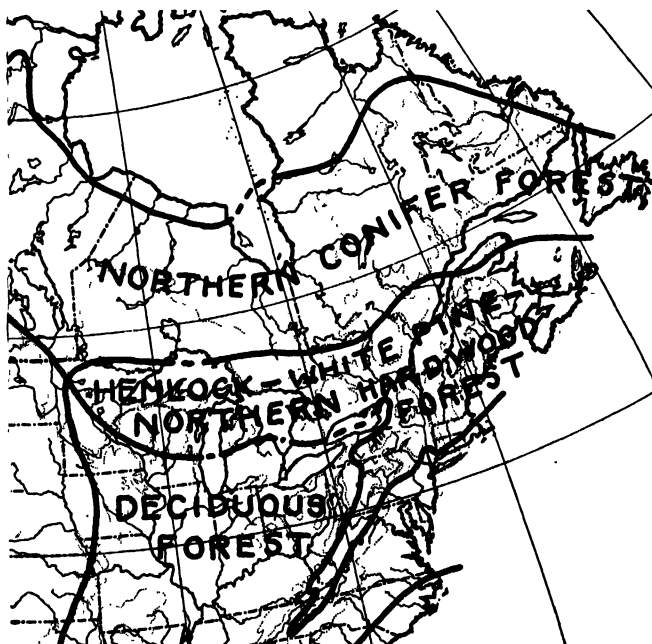


FIG. 4.   Map showing approximate limits of eastern hemlock region, as interpreted in the present paper.

its simplicity. It comprises scarcely half-a-dozen dominant tree species, chief among these being the balsam fir, *Abies balsamea*, white spruce, *Picea glauca*, black spruce, *Picea mariana*, and paper birch, *Betula papyrifera*.[2] Three other trees are frequently present, namely tamarack, *Larix laricina*, balsam poplar, *Populus balsamifera*, and aspen, *Populus tremuloides*. All of these trees are comparatively small in size and short-lived. Windfall is of common occurrence in the forest and often takes place simultaneously over considerable areas. Sprout reproduction is very largely absent. Small trees and shrubs are comparatively few in number, and layer societies of woody plants are poorly developed. The forest changes but little in its appearance from one season of the year to another. Mosses and liverworts commonly are abundant on the forest floor and often form a continuous carpet. The deciduous forest climax, on the other hand, is highly complex in its structure, varying greatly from place to place. It comprises a great wealth of tree species, all of which are deciduous—the so-called "hard-woods." Prominent among these are numerous oaks, *Quercus* spp., and hickories, *Hicoria* spp., chestnut, *Castanea dentata*,[3] tulip poplar, *Liriodendron tulipifera*, beech, *Fagus grandifolia*, sugar maple, *Acer saccharum*, white ash, *Fraxinus americana*, black cherry, *Prunus serotina*, basswood, *Tilia* spp., black birch, *Betula lenta*, yellow buckeye, *Aesculus octandra*, cucumber magnolia, *Magnolia acuminata*, and black walnut, *Juglans nigra*. Unlike the northern conifer climax, the dominant trees here are relatively large-sized and long-lived. Windfall is comparatively infrequent and, as a rule, quite local in its occurrence, being largely confined to single scattered specimens. The climax species, and especially certain ones, reproduce vegetatively by means of sprouts which originate from dormant or adventitious buds borne either at the base of the trunk or on surface roots. The forest tends to be several-storied, with one or more layer societies of shrubs and small trees. It exhibits marked variations in aspect at different seasons of the year. Mosses and liverworts are poorly developed on the forest floor, their growth here being hindered by the heavy accumulation of leaves which blankets the ground every autumn.

Forest conditions in the eastern hemlock region, as might be expected, are transitional in many ways between those of the coniferous forest region to the north and those of the deciduous forest region to the south. Large areas of country are occupied by evergreen coniferous forest and large areas by deciduous hardwood forest, while other large areas are forested with a mixture of conifers and hardwoods. But the forest vegetation also exhibits

[2] In general, the scientific names of tree and shrub species are given the first time they are mentioned. Thereafter they are referred to by their common names only. Sudworth's Check list ('27) is followed for the trees, and Gray's Manual (Robinson and Fernald '08) for shrubs and herbaceous plants.

[3] Previous to its near-extermination by the chestnut blight fungus, this was the most abundant tree species over large portions of the deciduous forest region.

certain features which are both unique and distinctive. As a result there exists not a little confusion or difference of opinion as to how this region should be treated in its relation to that of the two adjoining ones.

General accounts dealing more or less specifically and for the most part rather briefly with forest conditions and relations in the eastern hemlock region as a whole have been written by Transeau ('05, '23), Harshberger ('11), Frothingham ('15), Nichols ('18), Shantz and Zon ('24), and Weaver and Clements ('29); while for different parts of the region the following papers, among others, contain more or less detailed descriptions: for Nova Scotia—Fernow, Howe and White ('12) and Nichols ('18); for New England —Cooper ('22), Hawley and Hawes ('12), Nichols ('13), Hill ('23), and Lutz ('28); for Pennsylvania and New York—Bray ('15) and Lutz ('30); for eastern Ontario—Howe, White and Fernow ('13); for Michigan—Whitford ('01), Gates ('12), Harvey ('22), Gleason ('25), Kittredge and Chittenden ('29), Darlington ('31), McIntire ('32), and Westveld ('33); for Minnesota—Bergman and Stallard ('16), Lee ('24), Stallard ('29), Kittredge ('34), and Grant ('34).

The brief resumé and interpretation of forest conditions in the eastern hemlock region which follow are based in large measure on the writer's field observations over a period of about 25 years during which, at one time or another, visits have been made to practically all parts of this region situated east of Wisconsin.

## THE CLIMATIC CLIMAX FOREST OF THE REGION

The climax favored by climate and the one which is generally developed on the better soils throughout the eastern hemlock region, except where the natural conditions have been modified by fire or man, is a mesophytic forest comprising a mixture of evergreen coniferous and deciduous broadleaf trees. The more characteristic species concerned are hemlock, *Tsuga canadensis*, sugar maple, *Acer saccharum*, beech, *Fagus grandifolia*, yellow birch, *Betula lutea*, eastern white pine, *Pinus strobus*,[4] basswood, *Tilia glabra*, American elm, *Ulmus americana*, white ash, *Fraxinus americana*, red oak, *Quercus borealis*, black cherry, *Prunus serotina*, red spruce, *Picea rubra*, balsam fir, *Abies balsamea*, white spruce, *Picea glauca*, red maple, *Acer rubrum*, and Norway pine, *Pinus resinosa*.

In the position of relative importance which they occupy in the community, these trees differ greatly among themselves, both in different parts of the region and locally within the same general section. Sugar maple (fig. 5 *B*) is the most universally distributed, being seldom absent and commonly the most abundant tree; but hemlock (fig. 5 *D*) and beech (fig. 5 *C*)

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[4] The writer shares the opinion held by various others that *Pinus strobus*, the "northern" white pine of Sudworth ('27), is much more appropriately called the eastern white pine, by way of contrast with the western white pine, *P. monticola*, which, according to Sudworth's maps ('13), actually ranges farther north.

rival and even outrank the maple in abundance over large parts of their range. Taken together, in varying proportions, these three trees ordinarily make up the bulk of the forest. Yellow birch (fig. 5 G) is a consistent and usually a conspicuous member; but as a rule it is much less abundant than
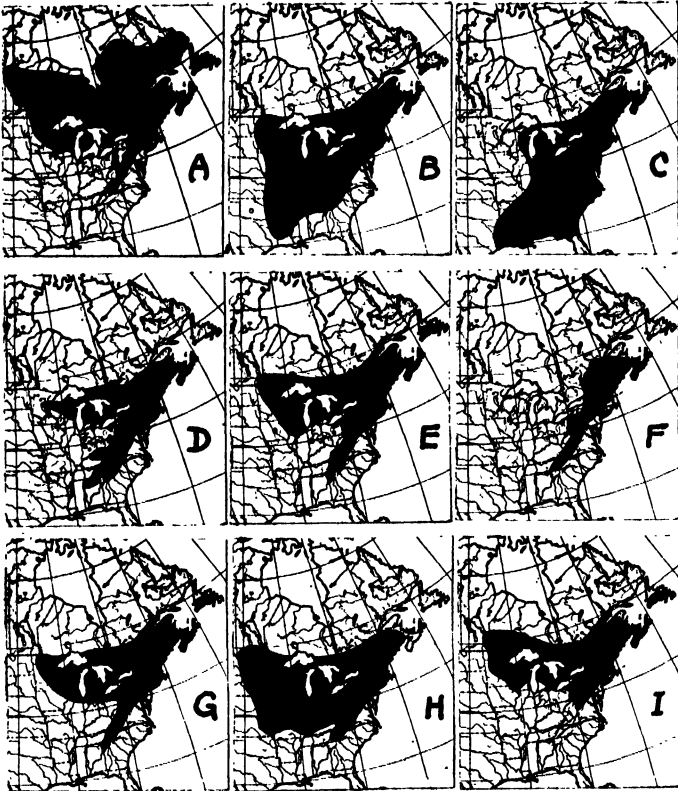


FIG. 5. Maps showing approximate distribution of the following characteristic trees of the eastern hemlock region: (A) Abies balsamea, (B) Acer saccharum, (C) Fagus grandifolia, (D) Tsuga canadensis, (E) Pinus strobus, (F) Picea rubra, (G) Betula lutea, (H) Tilia glabra, (I) Pinus resinosa.

the three preceding, except toward the north where it sometimes may be the dominant species. White pine (fig. 5 E), the ecological status of which is discussed on another page, is common throughout. Basswood (fig. 5 H) and elm, sparingly represented in the climax eastward, are much more extensively developed westward where, in the Lake States, Frothingham states that the two together comprise more than 20 per cent of the hardwoods. White ash and red oak are common throughout, while the black cherry is frequent, especially southward, occurring for the most part as scattered specimens. Red spruce is one of the dominant trees in the climax over considerable areas within its rather limited geographical range (fig. 5 F),

especially in the mountains of New York and New England; but this tree is not present at all in the Lake States. Balsam fir (fig. 5 *A*) and white spruce are variously represented in the climax toward the northern fringe of the eastern hemlock region, and the fir, according to Grant ('34), is the most characteristic climax conifer of this region in Minnesota. Red maple is usually present but only as a minor constituent. Norway pine, while one of the dominant trees over enormous tracts of country (fig. 5 *I*), occurs only rarely in forests of the climatic climax type. Its ecological status will be referred to again.

As in the deciduous forest region farther south, the climax forests of the eastern hemlock region commonly show a stratified structure, although there is much local variation in this respect. Among the small trees, striped maple, *Acer pennsylvanicum*, and mountain maple, *A. spicatum*, are seldom absent and frequently form a scattered under-story, with or without such other species as hop hornbeam, *Ostrya virginiana*, and alternate-leaved dogwood, *Cornus alternifolia*. The Canada yew, *Taxus canadensis*, and beaked hazelnut, *Corylus rostrata*, are common throughout most of the region, and the hobble-bush, *Viburnum alnifolium*, is abundant eastward. All three of these tall shrubs, and especially the yew, tend to form well-marked layer societies. Fly honeysuckle, *Lonicera canadensis*, and red elderberry, *Sambucus racemosa*, are common associates but lack the gregarious habit. Among the characteristic herbaceous plants, mostly of widespread distribution and often growing in considerable local profusion, may be mentioned in particular the following species: *Aspidium spinulosum, Lycopodium lucidulum, Lycopodium annotinum, Clintonia borealis, Smilacina racemosa, Maianthemum canadense, Streptopus roseus, Medeola virginiana, Trillium* spp., *Actaea* spp., *Oxalis acetosella, Viola* spp., *Aralia nudicaulis, Trientalis americana, Mitchella repens,* and *Aster acuminatus.*

As one of the striking features of the climax should be mentioned the luxuriant development of various corticolous mosses and liverworts, which commonly grow in dense masses on trunks of living trees and of sugar maple in particular. It seems not unlikely that this feature may be of considerable ecological significance in reflecting the influence of certain climatic conditions which are more or less peculiar to this region.

In its larger and more general aspects, the nature of the climatic climax forest of the eastern hemlock region is very much the same throughout. In its detailed local structure, however, and especially in the identity and relative abundance of the different tree and shrub species, it exhibits a considerable degree of variation, both in different parts of the region and locally in the same part. In the upper peninsula of Michigan, for example (see McIntire, '32), the Land Economic Survey has recognized four different associations of climax hardwoods alone, in addition to which may be distinguished associations of pure hemlock, and of hemlock and white pine, plus various combinations of conifers and hardwoods. These variants or

modifications of the larger climatically-determined community may or may not be of ecological import in reflecting the influence of local soil and topographic conditions; and much remains to be done in the way of investigating the relation between soils and forest vegetation in the light of modern soil science. But in the main, when looked at from the standpoint of regional plant geography, such variations would appear to be of relatively minor significance. From this standpoint the climatic climax as a practical working basis is most useful when interpreted broadly, to embrace a series of plant associations which may vary more or less widely among themselves in floristic composition, and to some extent also in ecological structure. Thus, in the eastern hemlock region, there is no one plant association which stands out, to the exclusion of all other associations, as being the climatic climax. The fact of outstanding ecological interest here is the widespread distribution, in one form or another and throughout the region, of climax forests which approximate and center around the hemlock–white pine–northern hardwood type.

## ECOLOGICAL STATUS OF WHITE PINE IN RELATION TO OTHER TREES IN THE CLIMATIC CLIMAX

In its geographical distribution (fig. 5 E) the white pine is very nearly coextensive with the region under consideration. Over much of this country it has stood out in times past as being economically the most valuable tree; over large areas it once formed pure or nearly pure stands. Then, as today, it was an important tree in the reclamation of abandoned farm lands and of burned or lumbered forest lands. But the white pine also very commonly grew in mixture with hardwoods and hemlock; in fact, it was here that this tree attained its finest growth and largest size. In the primeval wilderness of colonial days, "One may picture a forest in which broad-leaved trees and hemlock formed a dense stand from eighty to one hundred feet high, above which, either by small groups or single trees and varying greatly in abundance, white pines reached to a height of 150 feet or more" (Fisher, '33). But the ecological status of this tree in relation to the climatic climax is one which never has been satisfactorily established. Indeed it has been an open question whether the scattered pines towering above the general level of the primeval hemlock–hardwood forest of pioneer days should be regarded as bona fide constituents of the climax, being able to reproduce themselves on the forest floor, or whether, as Whitford ('01) and others would maintain, they represented merely relicts of an earlier successional stage, destined in course of time to give way completely to hemlock and hardwoods.

On a basis of observations in the Huron Mountains of northern Michigan, where at least one fine primeval stand of pine and hardwood still exists, as well as in other places, the writer has reached the following conclusions: (1) White pine, throughout a large part of its geographical range is a normal,

although minor, constituent of the climatic climax forest.    (2) As such, it occurs not as pure stands but in varying admixtures with hemlock and hardwoods.    (3) Where represented in such mixed growth by numerous trees of approximately even age, the origin of the pine characteristically dates back to a forest fire or to some other more or less widespread calamity; but (4) where represented here only by scattered specimens of uneven age, or only very locally, the pine in all probability has originated in relatively small forest openings brought about by windfall or by some other purely local influence.    Openings due to windfall and the like are to be looked upon as a normal incident in the life of the forest.    (5) Once established in openings of any description, the pine may or may not grow to maturity; to a varying degree, depending on local and seasonal conditions, it does so. Germinating in the forest, under favorable conditions of moisture and soil the white pine may be able to hold its own in competition with more tolerant trees by virtue of its persistent growth, its large size, and its great length of life.    One specimen examined by the writer in the Hurons measured 62 inches in diameter (at breast height) and probably was more than 500 years old.

In its relation to the climatic climax of this region, the position of the white pine is quite comparable with that occupied by tulip poplar in the southern Appalachians and by Douglas fir in the Pacific northwest.

PHYSIOGRAPHIC CLIMAX FORESTS IN THE EASTERN HEMLOCK REGION

Vast areas of country in the eastern hemlock region support climax forests of very different character from the climatic climax.    Two types in particular are widespread in their occurrence, resulting from the widespread distribution of soil conditions which discourage the development of the climatic climax.

Mixed stands of white pine, Norway pine and jack pine are especially characteristic of the Lake States where, in former days, they occupied large tracts of sandy land, apparently too dry for the development of the climatic climax.    It was in these so-called "pineries" that the white pine grew in greatest profusion, sometimes, according to Spalding and Fernow ('99), forming pure stands several square miles in extent.    But on the whole the pineries comprised a mixture, now one and now another of the three species being dominant, depending very largely upon local soil conditions.    Where developed on the better soils, forests of this description may represent a sub-climax due to fire; but under favorable conditions, in the course of succession, they give way here to forests of the climatic climax type already described, with hemlock and hardwoods becoming dominant, white pine assuming a comparatively subordinate position, and Norway pine tending to disappear completely.    On the poorer soils they represent a physiographic climax of a type which is peculiar to the eastern hemlock region.

Forests of balsam fir, black spruce, white spruce, northern white cedar, *Thuja occidentalis*, and tamarack, in varying admixtures, occupy large areas

of flat, poorly drained, and more or less swampy or semiswampy ground in the upper Michigan peninsula, in the plateau region of northern Maine, and elsewhere.    These physiographic climax forests closely resemble the climatic climax of the northern conifer region, of which they may be looked upon as being, in a sense, a southward extension.    In the eastern hemlock region, however, they are able to hold their own only in situations which are edaphically unsuited to forests of the climatic climax type.

Three swamp forest types characteristic of the eastern hemlock region are described by Hawley and others ('32) as "climax for the site" in which they occur, namely the black spruce type, the northern white cedar type, and the black ash (*Fraxinus nigra*)–American elm–red maple type.

### Ecological Status of the Eastern Hemlock Region

In a paper published many years ago Transeau ('05) advances the idea ' that eastern North America, north of the Gulf States, is occupied by two great forest centers, namely "the northeastern conifer forest, centering in the St. Lawrence basin" and "the deciduous forest, centering in the lower Ohio basin and Piedmont plateau."    He emphasizes the fact that "the St. Lawrence basin is a definite center about which is distributed an unique type of forest," a forest which, while floristically related to the forests of



FIG. 6.    Map showing distribution in eastern North America of "several of the dominant conifers of the northeastern conifer center," the relative intensity of shading indicating the relative number of species present in different parts of the region.    (After Transeau '05.)

other parts of the continent, is "ecologically and climatically . . . distinct." The region thus described coincides with the one under consideration in the present paper. But Transeau makes no distinction between this region, with its magnificent forests and unique assemblage of characteristic species, and the region farther north, with its low, more or less swampy woodlands of predominantly boreal trees. By way of illustrating his ideas, Transeau presents, among others, a map showing the "distribution of several dominant conifers of the northeastern conifer center," in which "the relative intensity of shading indicates the relative number of species found in the region." This map, herewith reproduced as figure 6, brings out in a very graphic manner the feature which Transeau wishes to emphasize, namely the comparative richness in conifer species of the region in question. It fails, however, to show one other very significant fact, namely that there are *two* centers of conifer distribution in northeastern North America, one for distinctly boreal species and another for the various less boreal species which are peculiar to the eastern hemlock region.[5]

This latter idea, extended to include hardwoods and also various trees of southward distribution, is well brought out by two accompanying maps, on one of which (fig. 7 A) the centers of north—south distribution for 23 trees are represented by a series of east—west lines. The species selected, for the most part, are representative constituents of the climatic climax forests in different parts of eastern North America, north of the Gulf States. Mapped in this way, it will be noted that they fall very clearly into three geographical groups, as follows: (1) a northern group, centering east-and-west in the region south of Hudson Bay and comprising the balsam fir, white spruce, black spruce, tamarack, paper birch, and balsam poplar; (2) a southern group centering east-and-west in the Ohio basin and region to the south, and including various species of oak and hickory, the chestnut, tulip poplar, beech, white ash, black birch, yellow buckeye, cucumber magnolia, and black walnut, together with numerous other trees of primarily southward distribution which have not been indicated on the map; (3) an intermediate group centering east-and-west in the great lake region and including the hemlock, white pine, Norway pine, yellow birch, sugar maple, and basswood. The second map (fig. 7 B), constructed in a similar manner but with the lines here representing northern limits of distribution for the species concerned, brings out essentially the same grouping.

Directing our attention now to the climatic climax trees of the eastern hemlock region, as listed on page 407, and considering these from the standpoint of their geographical distribution, it will be found that they fall into three or, perhaps better, into four groups, as follows: (1) trees whose centers of north—south distribution lie north of the region and which are widely

[5] Parenthetically it should be remarked that the United States Forest Service, in its latest map of the forest regions of the United States (Mattoon '33), as in earlier editions, includes the eastern hemlock region as a part of the "northern forest" region.

distributed northward, being constituents of the northern conifer climax, namely balsam fir and white spruce; (2) trees whose centers of north–south distribution lie within the region, whose range as a whole extends but little beyond it, and which are members of the climatic climax in no other region, namely hemlock, white pine, yellow birch, Norway pine (if this be regarded as a climatic climax tree), and perhaps red spruce; (3) trees whose centers of north–south distribution lie within the region or immediately south of
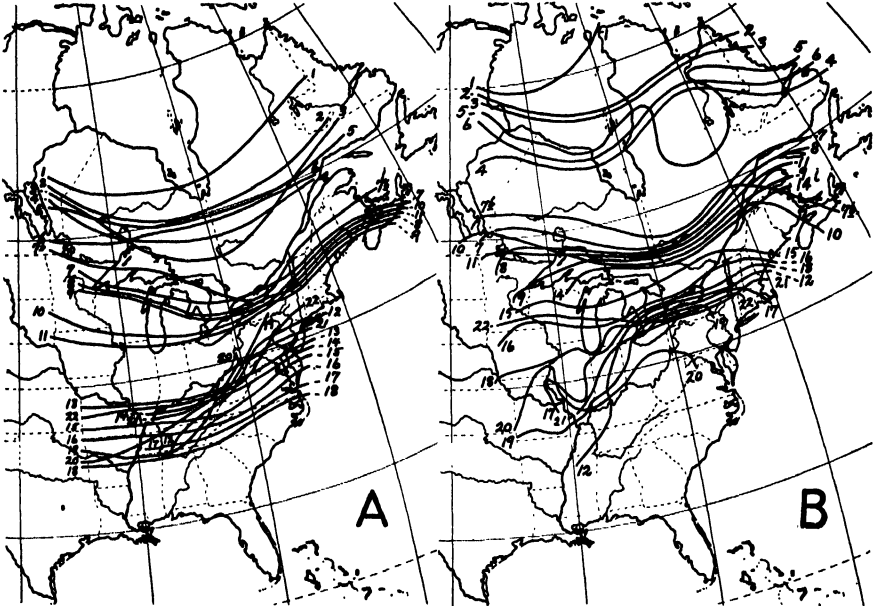


FIG. 7.   Maps showing (A) approximate centers of north–south distribution, and (B) approximate limits of northward distribution for various representative trees of the climax forests of eastern North America.  List of species as follows: (1) *Larix laricina*, (2) *Picea glauca*, (3) *P. mariana*, (4) *Abies balsamea*, (5) *Populus balsamifera*, (6) *Betula papyrifera*, (7) *Pinus strobus*, (7b) *Pinus resinosa*, (8) *Betula lutea*, (9) *Tsuga canadensis*, (10) *Tilia glabra*, (11) *Acer saccharum*, (12) *Castanea dentata*, (13) *Fraxinus americana*, (14) *Fagus grandifolia*, (15) *Quercus alba*, (16) *Quercus velutina*, (17) *Liriodendron tulipifera*, (18) *Carya alba*, (19) *Magnolia acuminata*, (20) *Aesculus octandra*, (21) *Quercus montana*, (22) *Juglans nigra*.

it, but which range well to the south, there entering more or less into the composition of the deciduous forest climax, namely sugar maple, basswood, and probably the northern red oak; (4) trees whose centers of north–south distribution lie far to the south and which are widely distributed southward as constituents of the deciduous forest climax, namely beech, white ash, black cherry, and perhaps American elm.

In its bearing on the ecological status of the eastern hemlock region, it seems a significant fact that the first, or most northerly, of these four geographically-defined groups of trees occupies a position of relatively minor

importance in the climatic climax, as compared with the other three.    To
be sure, climatic conditions favor the growth of balsam fir and white spruce
over a large part of the eastern hemlock region, except toward the south,
and these two trees are widely distributed and often abundant in areas not
occupied by the climatic climax.    But as members of the climax itself they
are pretty much confined to the more northerly portions of the region, and
even here they are overshadowed by various other trees.    Along the coast
of northern Cape Breton, for example, both balsam fir and white spruce are
usually abundant as pioneers in abandoned pastures and elsewhere; as
second-growth woodlands they dominate the landscape on every side.    But
this condition is only temporary, for in the course of time they are destined
to be superceded, very largely at any rate, by northern hardwoods and hem-
lock.    Balsam fir in this region frequently reproduces itself in forests of the
climax type but seldom grows to maturity.    White spruce, being relatively
intolerant of shade, only occasionally establishes itself on the forest floor.
In varying degree, and as elsewhere indicated, it is the trees of the three
more southerly groups which make up the bulk of the climatic climax forest
throughout the eastern hemlock region.    When growing in competition with
balsam fir and white spruce on the better soils, these trees are equipped to
gain the ascendency by virtue of their longer life and greater size, coupled,
among other things, with the remarkable capacity of hemlock, sugar maple
and beech in particular to reproduce and grow in the shade.    From an
ecological point of view, therefore, these and various other features of the
climatic climax combine to set the eastern hemlock region apart as being
distinct from the northern conifer region.

Very different is the relation between the region under consideration
and the deciduous forest region farther south.    Historically it is of course
from the south that the present-day flora of the eastern hemlock region has
been derived.    As the writer has expressed it in an earlier paper ('18), "this
region represents a great tension zone in which competition between the
northern and southern climax trees is still in active progress. . . . The
nature of the climax forest, taken in its entirety, is intermediate between
that of the evergreen coniferous and that of the deciduous climatic forma-
tion. . . . Nevertheless, largely because of the almost universal supremacy,
in situations edaphically favorable to their development, of the climax trees
of the deciduous forest formation over those of the northeastern evergreen
coniferous forest formation, wherever these two groups come into competi-
tion with one another, from the standpoint of ecological plant geography
it seems best, on the whole, to regard the vegetation of this transition region
as constituting merely the northward extension of the deciduous forest
formation."    Speaking along this same general line and with reference more
especially to conditions in the southern Michigan peninsula, Harvey ('19)
says: "It is contended upon ecological grounds that any region should be
classified upon the basis of the highest ecological type which may find ex-

pression therein. Upon this basis the southern peninsula should then be considered as a northern extension of the deciduous climax forest formation. . . . Our region thus represents a great tension zone in which the northern outposts of the deciduous climax forest formation and the southern relicts of the northeastern evergreen forest formation overlap and intermingle. . . ."

In the same paper referred to above (Nichols '18), the author remarks to effect that "while, from the floristic point of view, the vegetation of this region certainly is more or less unique, from an ecological point of view it is doubtfully to be regarded as a distinct climatic formation." Yet a great deal may be said in favor of this very view—of treating the eastern hemlock region as an ecological unit distinct from the deciduous as well as from the northern conifer forest region. Attention has already been called to the remarkable group of "endemic" trees which is found here; also to the fact that here, more than in any other section of eastern North America, the climatic climax tends to be dominated by intensely mesic trees of pronounced shade-enduring capacity. The hemlock, in its ecological characteristics, closely resembles the sugar maple, and the density with which the seedlings of these two trees may carpet the forest floor, to one who has never seen it, seems almost unbelievable. The woody and herbaceous undergrowth of the forest likewise is strongly mesic and sciaphilous, comprising a distinctive assemblage of species which recurs with remarkable constancy throughout most of the area. To be sure the climax forests of this region have many features in common with the deciduous forest region, in particular the mutual dominance over large areas of deciduous trees. And yet it may not be without significance that the outstanding trees of the climatic climax here, with the single exception of the beech, belong to groups 2 and 3, as outlined above—species in which the centers of north–south distribution lie either within the region or immediately to the south. As compared with the climax deciduous forests farther south, there is a conspicuous absence here of oaks (only one species being at all important), hickories, tulip poplar, chestnut, and other relatively southern hardwoods, as also of certain forest shrubs and small trees. Not without significance also may be the fact that in Connecticut and elsewhere along the southern borders of this region the hemlock and northern hardwoods gain successional ascendency over oaks and other relatively southern trees when competing with them on the better soils; whereas in the heart of the region the succession may be dominated from start to finish by trees which are more or less "endemic."

Of not a little interest in this present connection are the two maps shown in figure 8. These are based on the range maps of figure 5 and represent an attempt to portray, by means of differential shading, the relative species-abundance of certain groups of trees in different parts of eastern North America. Each of these maps was made by photographically superimposing
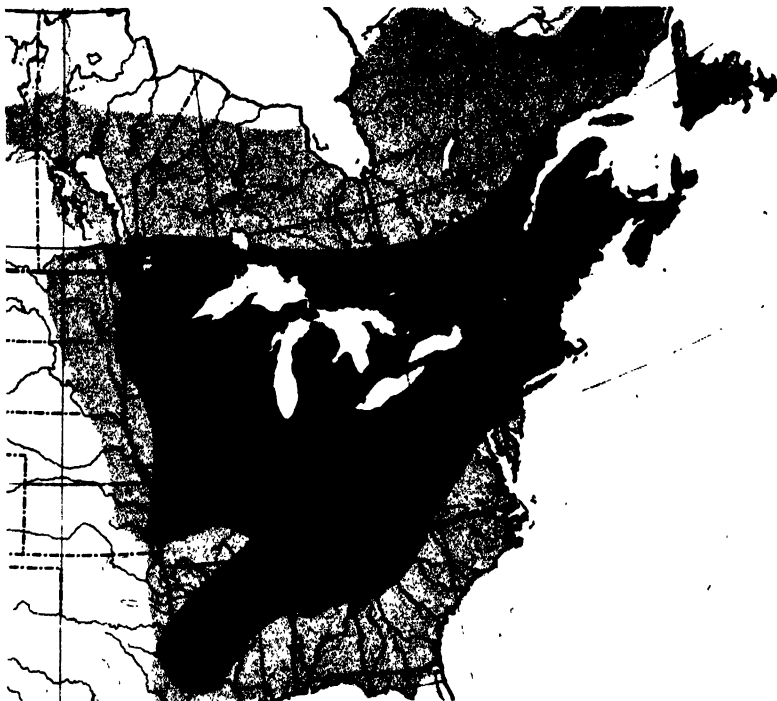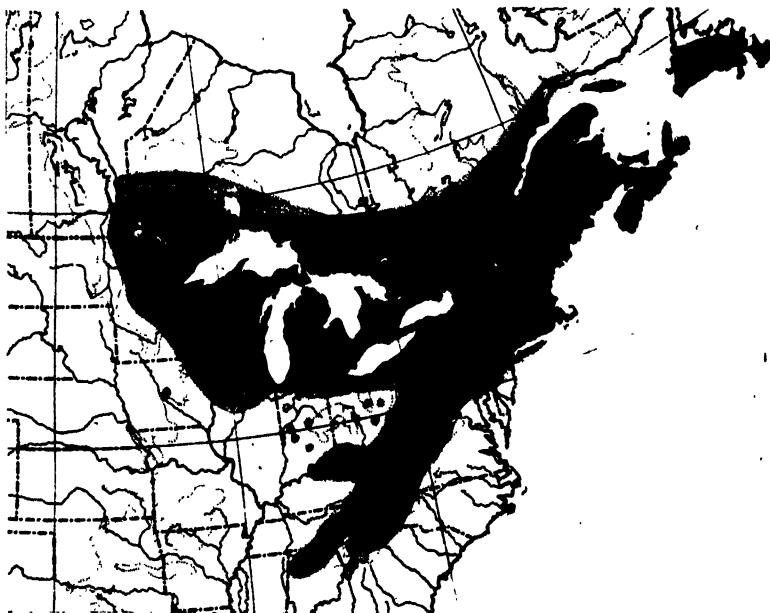
FIG. 8. Maps showing region of greatest concentration (A) for all species shown in figure 5, with exception of *Pinus resinosa*, (B) for the following four species: *Tsuga canadensis*, *Pinus strobus*, *Pinus resinosa*, and *Betula lutea*.

several of the individual range maps to form a single composite or collective range map for the entire group of species concerned, the number of species represented in any given locality being of course proportional to the depth of shading. Made in this way, figure 8, map $A$, combines the ranges of the following seven trees: balsam fir, sugar maple, beech, hemlock, white pine, yellow birch and basswood. Similarly figure 8, map $B$, combines the ranges of the four "endemic" species, hemlock, white pine, yellow birch, and Norway pine. In a manner which is unmistakable, these maps reveal the eastern hemlock region as the area of greatest concentration for the two groups of trees concerned.

Weaver and Clements ('29), in characterizing the climatic climax of this same general region (but delimited as in figure 3), describe the "lake forest" formation as consisting of a single association in which white pine, Norway pine and hemlock are the climax dominants. While unable to agree with these authors in regarding Norway pine as one of the dominant trees in the climatic climax, there can be little question that the position of prominence which these three conifers occupy in the general vegetation furnishes one of the strongest reasons for recognizing the hemlock–white pine–northern hardwood forest of eastern North America as an autonomous vegetation unit.

Brief attention should be called to the vegetation maps of Shreve ('17) and of Shantz and Zon ('24) in which the eastern hemlock region, as here delimited, is shown to be occupied by three different types of vegetation, variously distributed, namely (according to Shantz and Zon) spruce–fir forest, jack pine–Norway pine–white pine forest, and birch–beech–maple–hemlock forest. According to their treatment in the present paper, the first two of these types represent physiographic climaxes and the third one the climatic climax of the region. This apparent discrepancy is explained by the different point of view maintained by these authors. According to Shreve, for example, in constructing such a vegetation map "the influence of soil character . . . must be ignored . . . ; the vegetation recognized for each region is the areally predominant plant-covering of the average upland . . . ; the so-called climax vegetation is a theoretical concept which cannot be applied to all regions and has little relation to the areally predominant vegetation even in regions where it can be demonstrated." The factuality of the last statement is at least open to question. In the opinion of the writer the climatic climax not only represents an almost indispensable criterion in ecological studies dealing with the vegetation of a particular region; it also constitutes the most valuable single index in ecological comparisons of the vegetation of different regions.

In conclusion it is of interest to note that the three forest regions recognized in this paper correspond roughly in their geographical limits with three of the temperature provinces distinguished by Thornthwaite ('31) on the basis of temperature efficiency, in his classification of the climates of

North America (see fig. 9). The northern conifer region corresponds with his Taiga temperature province, characterized by inadequate temperature efficiency; the eastern hemlock region with his Microthermal temperature



FIG. 9. Map showing temperature provinces of northeastern America distinguished by Thornthwaite ('31) on the basis of temperature efficiency.

province; and the deciduous forest region with his Mesothermal temperature province. A similar correspondence might be noted with the climatic regions distinguished by certain earlier authors. The dotted line in figure 9 indicates the position of the line between the microthermal and mesothermal provinces, as fixed by Kendall ('35).

## SUMMARY

The region under consideration, centering around the Great Lakes and the St. Lawrence basin, lies between the northern conifer forest region to the north and the deciduous forest region to the south. The climatic climax forest comprises a mixture of evergreen coniferous and deciduous broadleaf trees.

Considered with reference to their geographical distribution, these trees fall into four groups, as follows: (1) species whose centers of north–south distribution lie north of the region and which are widely distributed north-

ward, being constituents of the northern conifer climax, namely the balsam fir and white spruce; (2) species whose centers of north–south distribution lie within the region, whose range as a whole extends but little beyond it, and which are members of the climatic climax in no other region, notably the hemlock, eastern white pine and yellow birch; (3) species whose centers of north–south distribution lie within the region or immediately south of it, but which range well to the south, there entering more or less into the composition of the deciduous forest climax, notably the sugar maple and basswood; (4) species whose centers of north–south distribution lie far to the south and which are widely distributed southward, as constituents of the deciduous forest climax, among others, the beech and white ash.

From an ecological standpoint this region has commonly been treated as a part of the northern conifer forest region, but it differs from this more especially in the comparatively minor importance in the climax of the trees of group 1, as above described. It is much more closely related to the deciduous forest region, which it particularly resembles in the prominence of the trees of groups 3 and 4 in the climax.

Much may be said, however, in favor of treating this region as a distinct ecological unit, in itself. In addition to the climax species of group 2, numerous other trees and shrubs are prominent in the vegetation here which not only are more or less "endemic" but also are distinctive in their ecological characteristics. Also, various southern hardwoods are conspicuously absent here and, when present, tend to become replaced, in the course of succession, by hemlock and northern hardwoods.

White pine is to be regarded as a normal, although minor, constituent of the climatic climax; but Norway pine is very doubtfully a member in any sense.

Several physiographic climax types of forest are both of widespread occurrence and more or less peculiar to the region, of especial importance being the mixed forests of white pine and Norway pine, with or without jack pine, which constitute the so-called "pineries" of the Lake States.

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# THE PRAIRIE PENINSULA [1]

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One of the outstanding characteristics of Professor Cowles' lectures thirty-five years ago was his clear presentation and impartial appraisal of diverse conclusions regarding the origin and development of vegetation, and the factors involved. His discussions of diverse modes of approach and seemingly antithetic points of view have been a potent factor in the rapid development of plant ecology, and in particular the delineation and explanation of the vegetation of the Central States.

The interpretation of the " Prairie Peninsula " and its relation to the forests, which penetrate and partially encircle it, is a striking example of the value of diverse points of view. To some it has seemed to be not really prairie but rather deciduous forest with trees absent because of ecological conditions long since terminated and the forest scars kept open by human intervention, " since " the present climate is not different from that either north or south of it. Some have held that the scars would long ago have disappeared but for the unfavorable soil conditions—deficient drainage and poor aeration. To these the vegetation types of " mature soils " are forests, and the prairie is an expression of " immature soils." To still others the Prairie Peninsula represents a pyropyrrhic victory of the Indians and pre-Indians attempting to enlarge the native pastures, or to capture their grazing meat supply. This view had the backing of many prairie-born settlers to whom the fire peril and the treelessness were the only striking features of the prairie. In contrast there have been those who doubt that prehistoric climates are wholly responsible, and have persuaded themselves that the present climate, especially the precipitation and evaporation, is perhaps sufficient to account for the Prairie Peninsula and the forest vegetation that lies north, east and south of it. Details of these and still other points of view may be found in the papers of Shimek ('11, '25), Weaver ('34), Sampson ('21), Schaffner ('26) and Gleason ('22) who have made the major contributions to the study of prairie vegetation.

It is the purpose of this paper to locate more accurately the eastern extension of the prairie at the time of settlement, and to assemble the observations and problems which either directly or indirectly will be cleared up when we have a satisfactory group of explanations for the origin, development and

maintenance of the Prairie Peninsula. (fig. 1.) Any complete interpretation will account for the following:

1. The southern and southwestern boundary of the northeastern conifers —the pines, the spruces and the balsam fir, arbor vitae, and tamarack—extends variously from Minnesota southeastward to Pennsylvania, West Virginia and Kentucky. All of these species were common in early postglacial times throughout the states of the Prairie Peninsula as shown by fossil records, and some occur much farther south in the eastern states at the same elevation. (figs. 14, 16, 17, 24.)

2. The northern limits of the natural distribution of the scrub, pitch, and shortleaf pines, the sweet gum, certain oaks and other species that grow well when planted a hundred or more miles farther north, and which often occur much farther north in the Eastern States at both high and low elevations. (figs. 18, 20, 22, 23, 25–28.)

3. The characteristic absence of red maple as an *important* species in the bottomland forests of the corn belt streams, although abundant and characteristic of these situations both to the north and to the south.

4. The western limits of the mesophytic deciduous trees such as beech, tulip, chestnut, magnolia, and the evergreen hemlock. (figs. 12, 13, 15, 19.)

5. The occurrence of a distinctive prairie flora and isolated typical prairie communities as far east as northwestern Pennsylvania, as far north as central Wisconsin and Michigan, and as far south as Kentucky and Tennessee. (fig. 1.)

6. The absence of trees and the presence of prairie communities on both uplands and lowlands, on thoroughly drained *as well as* poorly drained areas from central Ohio to western Iowa. Many of the discussions of the causes of prairie and the absence of trees have dealt with one or the other of these situations. An adequate explanation should account for both.

7. The forests bordering and to some extent penetrating the prairie peninsula are regularly oak, oak-hickory, and oak-maple-linden and these borders are often miles in width, even in Indiana and Ohio, where much of the upland is otherwise occupied by beech-maple.

8. There is an almost complete absence of prairie openings in beech-maple forest regions. In central Ohio, to the east of the recent prairies, there are scattered small areas now occupied by beech-maple whose soil profiles indicate prehistoric prairie sites.

9. In Ohio the irregular boundary of the large central oak-hickory and prairie region crosses stream courses, high and low elevations, moraines, post glacial pre-erosion and erosion topography, diverse underlying shales and limestones, glacial and alluvial sands, gravels and clays. At some point the boundary between it and the beech-maple may lie on any one of these sites but elsewhere it veers to another, and edaphic factors are apparently of minor importance. The prairie areas themselves are mostly on flat upland, in shallow valleys, on broad upland knolls, on every local soil type, with textures

Fig. 1. The Prairie Peninsula with outliers. West of Ohio the areas were compiled from many published sources. The prairies of Indiana were mapped by Dr. R. B. Gordon, and the Barrens of Kentucky by Dr. S. N. Dicken.

ranging from gravelly loam to acid clay. There certainly is no relation be-
tween prairie areas and preglacial drainage lines. Since the time of the orig-
inal land surveys (about 140 years) very little change has taken place in the
border forests. Excluding planted groves there is no evidence that the beech
has moved at all. The sugar maple has moved only a few miles up certain
stream valleys and only in one locality has it invaded the oak-hickory on the
upland. In other words the vegetation of this great tract of land covering
3500 square miles has been in stable equilibrium for a long period of time.

10. The presence of deep prairyerths of both the upland and lowland
types testify to the long continued occupancy of prairie vegetation as far east
as central Ohio. Some of these areas of upland have been occupied in pre-
historic and historic times by oak-hickory forests; and some of the lowland
areas are now covered by bur oak, oak-hickory, and by various phases of the
swamp forest.

11. Certain deep soil profiles in the Mad River Valley (Ohio) show the
existence of shallow lakes for centuries during which algal concretions (some
a foot in diameter) and shell marl accumulated to a depth of several feet fol-
lowed by an accumulation of peat, and this in turn by a foot or two of prairie
soil. At the time of settlement these areas supported a mixture of relict bog
plants and wet prairie species, or swamp forest.

12. Relict communities of prairie plants in Ohio are now confined mostly
to areas known to have been prairie when these lands were settled a century
ago. Prairie colonies do not here invade and become established in the sec-
ondary successions on adjoining denuded and abandoned forest areas as read-
ily as they do in the Illinois and Iowa prairie regions.

13. The dominance, stability, and persistence of the tall-grass associations
must involve more than microclimatic and edaphic factors, since they cover
areas in nine states totalling about 90,000 square miles (east of a line drawn
from the west side of the " Big Woods " of southern Minnesota to Fayette-
ville, Arkansas) not counting the main body of the prairie (about 160,000
sq. mi.) which extends from Manitoba nearly to the Gulf.

14. The gradual decrease in the amount of invasion of former prairie
areas by forest communities as one passes from Ohio to western Iowa. In
Ohio such invasions have occurred to some extent on all topographic situations
while in western Iowa natural invasion has been more restricted to valley bot-
toms and slopes and upland stream margins. Weaver has recently shown the
great stability of the prairie at the western end of the peninsula. In central
Illinois its stability is only slightly less marked. In Indiana and Ohio its per-
sistence and return on abandoned areas is certainly less. But even here it has
only recently been exterminated from roadsides through the activities of the
relief " work projects."

15. There is no consistent correlation between the distribution of local
prairie or forest communities, and local soil types as classified by modern
pedologists, when large areas of the peninsula are studied. Likewise there

is no major difference in persistence on land lying west of the larger streams in contrast to the land east of streams (wind and fire factors).

16. The most isolated prairie remnants beyond the margins of the major prairie regions occur on bluffs, hill tops, cliff edges, sandstone outcrops, prehistoric and modern sand plains and dunes, rapidly eroding limestone out-. crops, and limestone with underground streams, as well as ponded areas, bog and marsh land.

17. The tall prairie grasses did not "come out of the deciduous forest" and they probably did not cross the Alleghany mountains, but reached the eastern seaboard by way of the New York State lowlands and the ancient southern coastal plain. From there they have followed up many of the rivers to the eastern slopes of the Alleghanies.

18. There is no need to go back to pre-Wisconsin epochs to account for any of the prairie communities in Ohio. It is quite possible that some of the prairies south of the glaciated region had developed before the last glaciation, but neither criteria nor substantial evidence have been published that differentiates them from the recent prairies. Likewise there is no evidence that a dry period caused the retreat of the last ice sheet, nor is there satisfactory evidence for an *early* postglacial xeric period. There seems to be more evidence to the contrary.

19. The almost complete absence of bog relict communities within the peninsula cannot be laid to absence of depressions or other suitable sites. At the eastern edges they were frequent at the time of settlement in shallow depressions, valley heads and about ponds and cold springs.

20. Using as a standard the species list of the excellent recent "Monograph" by Weaver and Fitzpatrick ('34), the proportion of species on the prairies of Ohio compares with those of the Prairie Center as follows:

Of the 11 major grasses .......................... 100%
 "   "  22 minor lowland grasses .................... 73%
 "   "  67 lowland flerbs ............................ 84%
 "   "  25 minor upland grasses ..................... 58%
 "   "  75 upland flerbs ............................ 40%

As the upland prairies of the "Monograph" contain many plains species it is not surprising that at the tip of the Peninsula the composition of upland prairies differs floristically more widely than that of the lowlands.

21. The prairies of the Peninsula exhibited the same associations as those defined by Weaver for the Prairie Center. There is no gradual change of dominants or of important species such as would be expected if the Peninsula were "transition grasslands." If there were a word "abruption," it would be far more applicable than "transition." The prairie-forest relationship was that of a mosaic of prairie and forest communities and the only transition was the forest border, at most a few rods in width. The presence of plains species in western Iowa should not be considered evidence that they represent a "plains transition," neither should the presence of some forest species far-

ther east make these "transition prairies." If we adopt this "transition" point of view then all our eastern forest types are really transitions.

To help in evaluating and explaining this summary of observations, the following comments are offered regarding the factors involved.
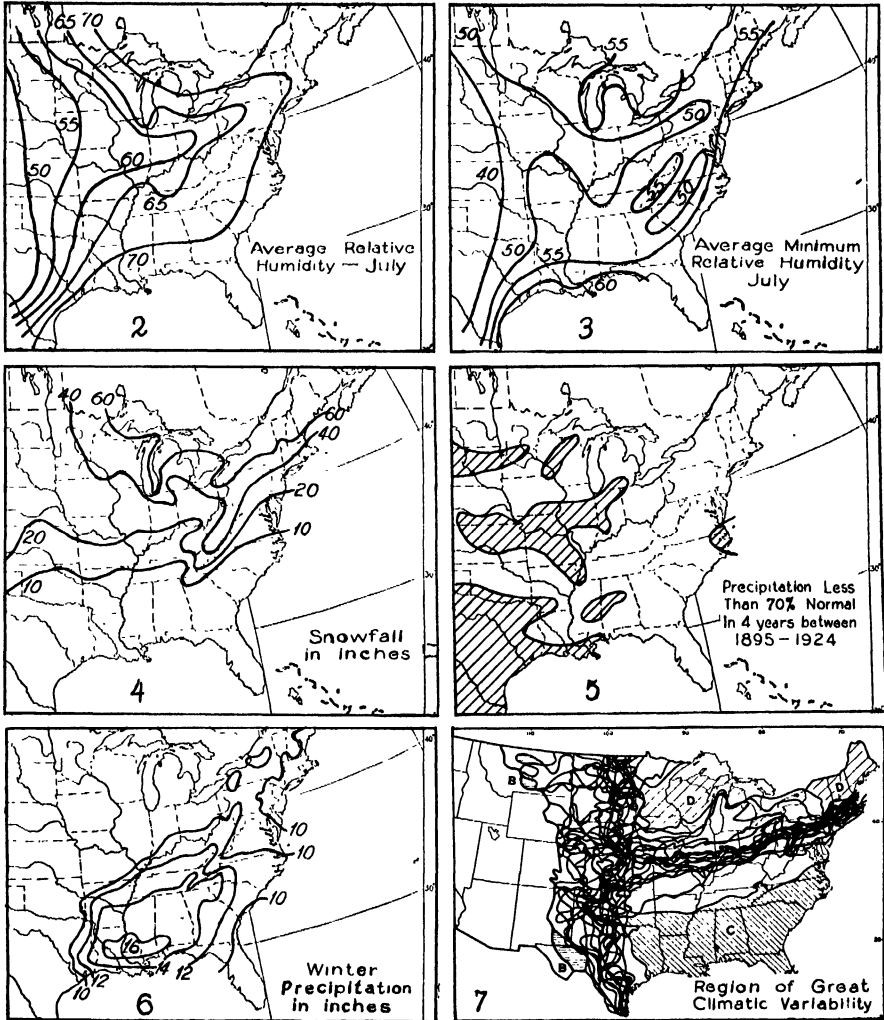
FIGS. 2, 3.  Low humidity of the midsummer season, an important factor in the prairie.

FIG. 4.  Snowfall, an important factor in the maintenance of the northeastern conifers.

FIG. 5.  Areas of deficient precipitation in a 20-year sample, 1895–1924.

FIG. 6.  Winter precipitation, an important factor in the southeastern forests.

FIG. 7.  Composite of 18 successive "year-climates" by Dr. H. M. Kendall. Reprinted from the January 1935, *Geographic Review* through the courtesy of the American Geographical Society of New York.  The other maps are from the *Atlas of American Agriculture*.

1. The annual and seasonal precipitation-evaporation ratios are undoubtedly lower in the Prairie Peninsula than in adjoining forest regions both north and south. During the thirty years since attention was called to the value of these ratios as *indices* of climatic differences over large regions not much progress has been made in securing standard evaporation data that can be
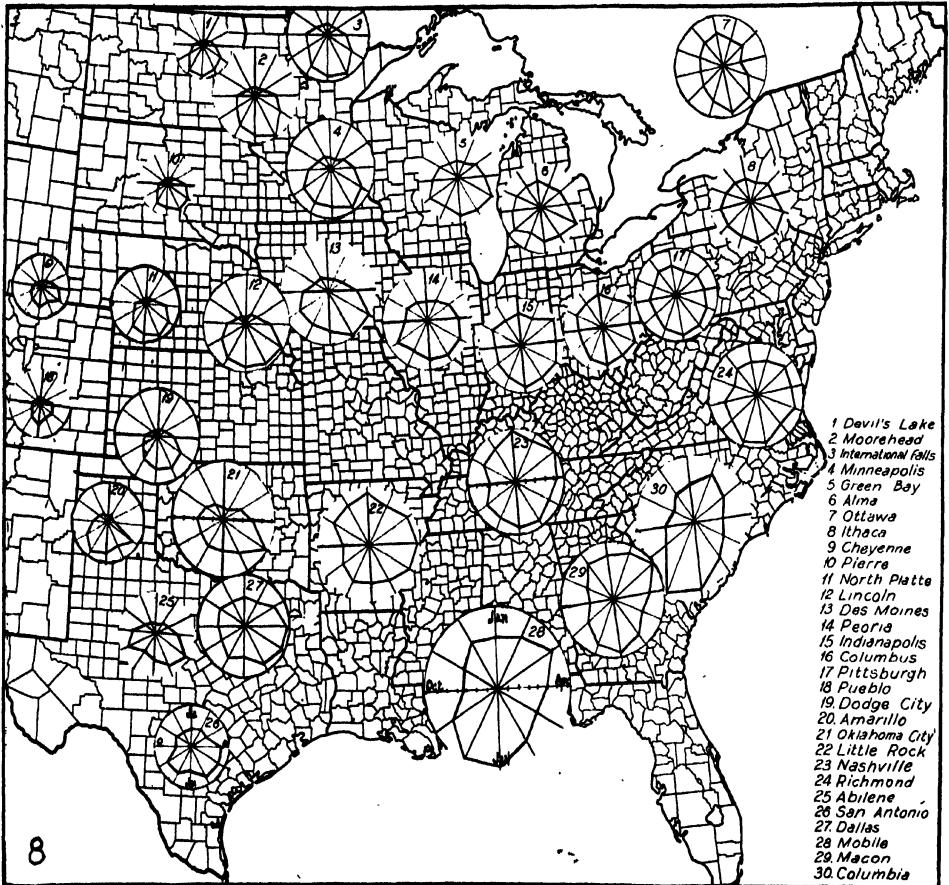


FIG. 8. Annual precipitation patterns in the eastern United States. The growing season lies below the horizontal axis of the polar charts. Note the effect of the Gulf Storms on winter precipitation, and the equalization of the average monthly rainfall.

compared with rainfall. Atmometers are valuable in studying local habitats, but the data they furnish cannot be compared with precipitation figures. The Weather Bureau has never been interested in setting up a network of "pan" stations that would provide these valuable data. Obviously, these ratios were never supposed to be applicable in local studies.

2. The midsummer relative humidity is certainly lower in the Peninsula than north and south of it as shown in figures 2 and 3.

3. The precipitation of the prairie region occurs largely during the growing season (fig. 8), and as we go from the Prairie Center eastward the proportion falls from about 75 per cent to about 50 per cent. The line of forty inches of average snowfall approximates the average boundary of the northern conifers (fig. 4).
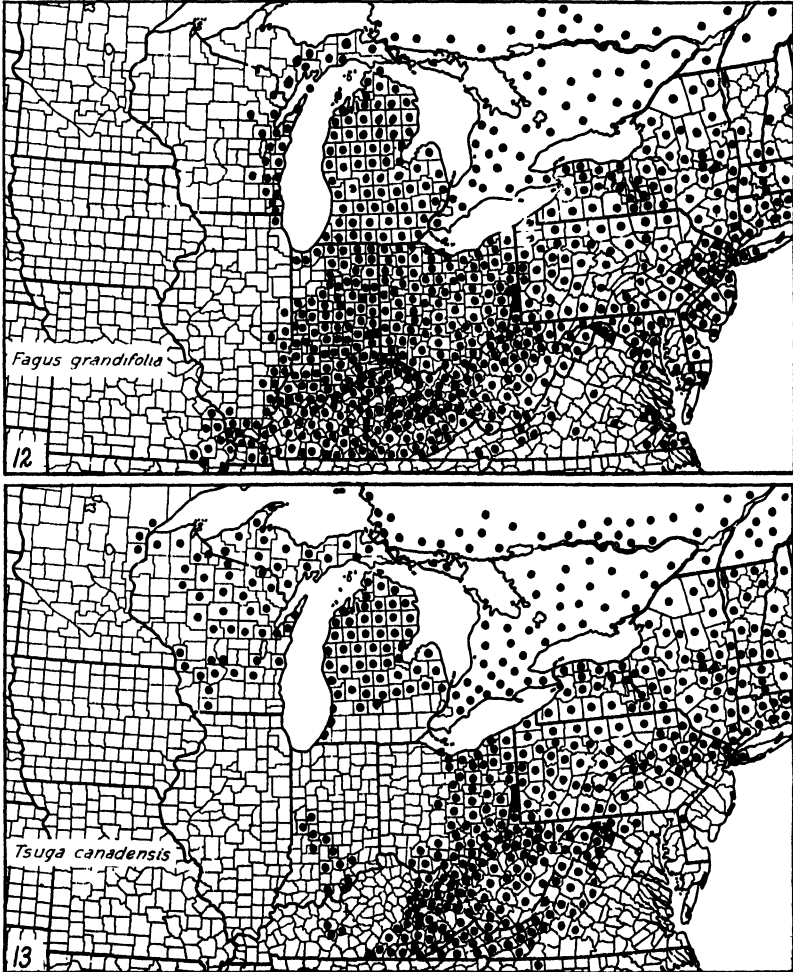


Figs. 12, 13. Western limits of the beech, *Fagus grandifolia,* and the hemlock, *Tsuga canadensis,* mesophytic species common in the northern deciduous forest formation. Beech is usually local in counties containing prairies.

4. The precipitation in successive months is more irregular in the tall-grass prairie, including the Peninsula, than in the mixed forests north and east. In the forests south-eastward, the irregularity is just as striking, but

Lincoln, Neb.

DesMoines, Ia.

Peoria, Illinois

Columbus, O.

Dormant Season

Growing Season

1910 1911 1912 1913 1914 1915
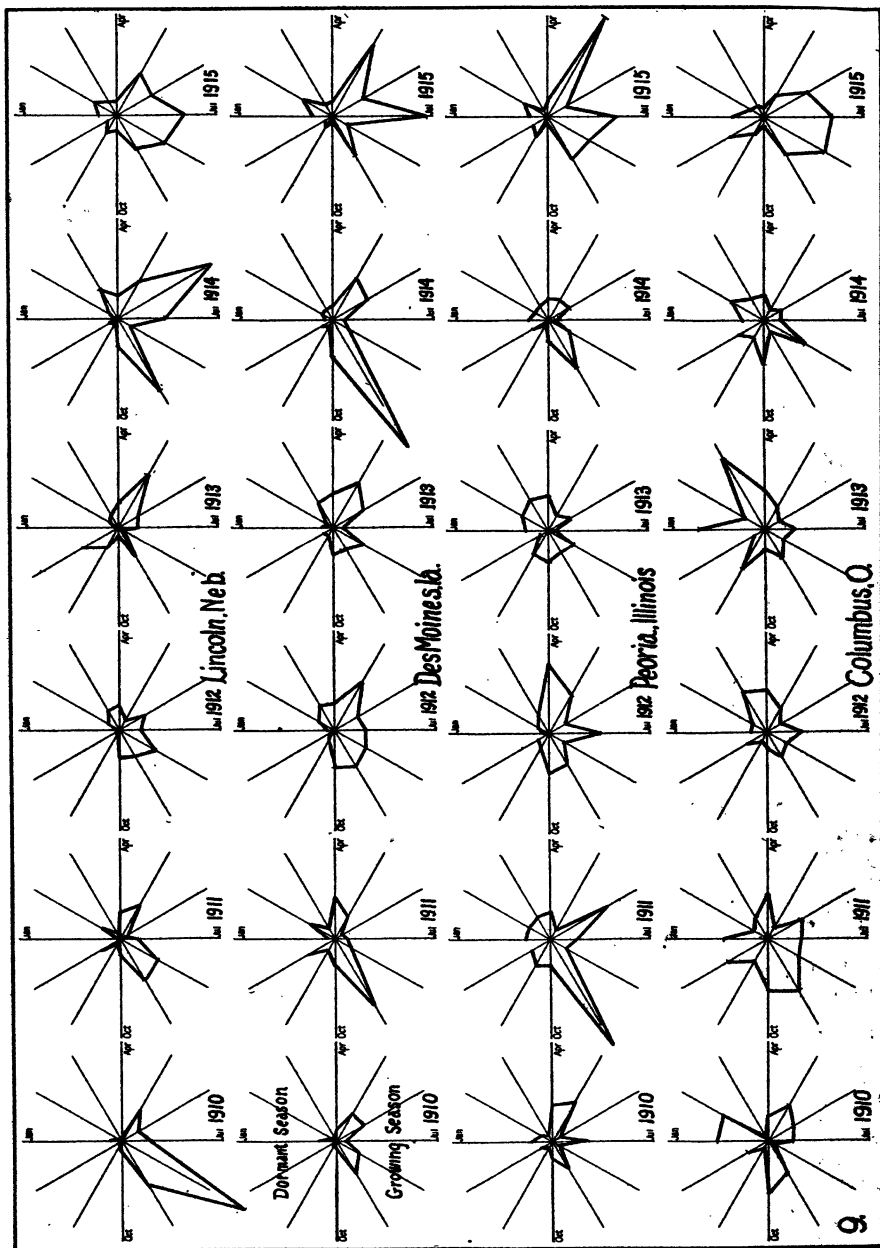
FIG. 9. Six-year samples of successive annual precipitation patterns at four stations in the Prairie Peninsula, showing variability in successive months and years. Note on the Peoria, Ill., record the low precipitation from November 1912 to May 1915. Compare records with those of figs. 10, 11.
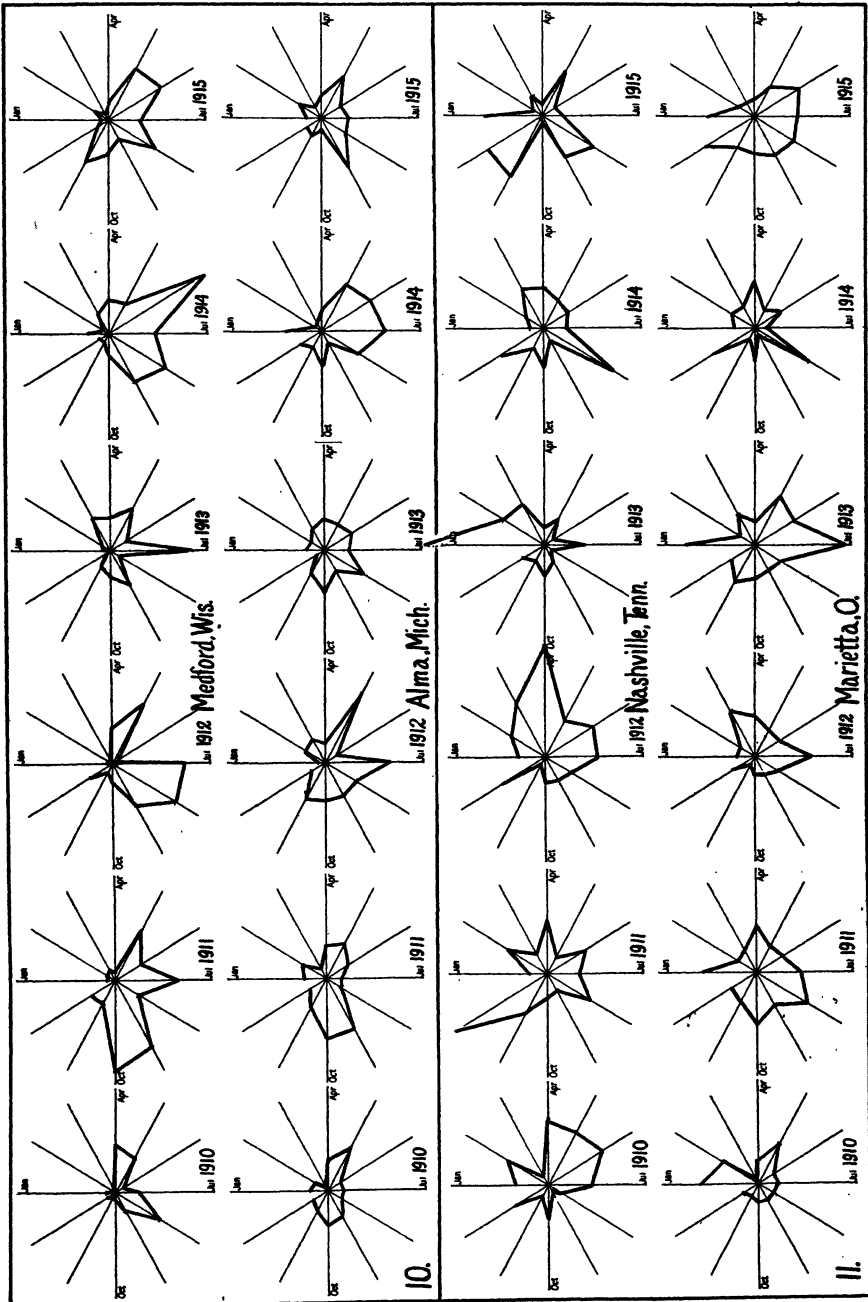
FIGS. 10, 11. Six-year samples of precipitation patterns of two stations northeast, and of two stations southeast of the Prairie Peninsula. Northeast the variations occur mostly during the growing season; southeast during all seasons. The scale in inches: each radius equals 10 inches.

the winter precipitation at least equals and sometimes exceeds the summer rains, so that accumulation of water in the soil takes place at all seasons (figs. 9, 10, 11).
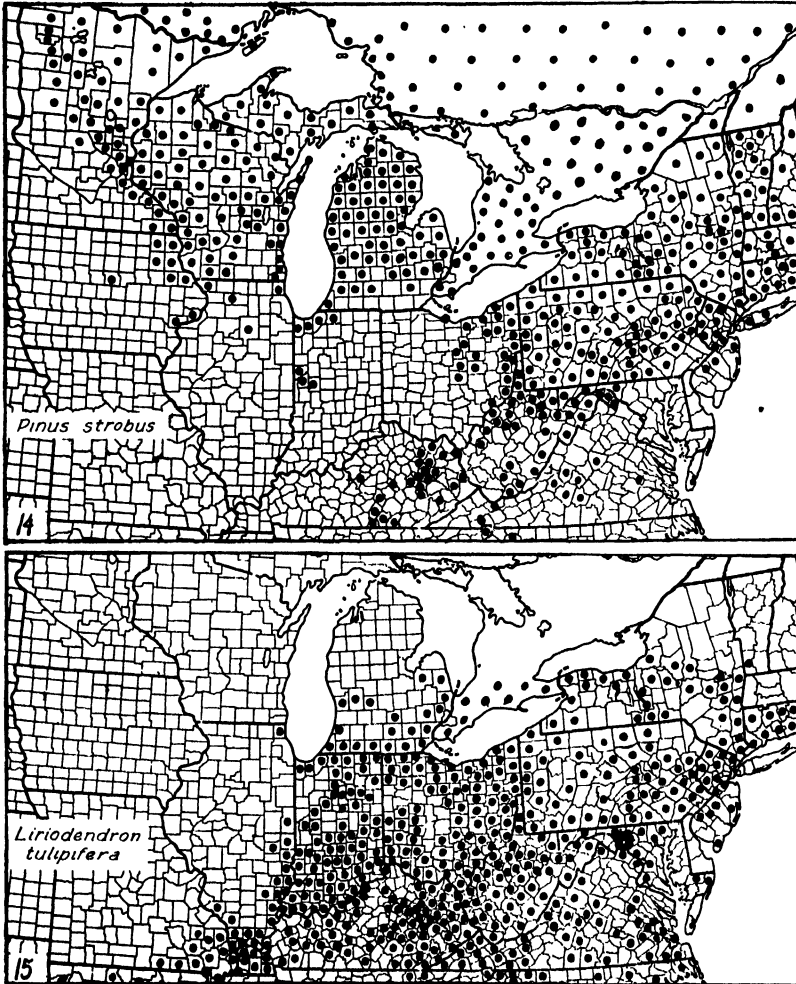


Figs. 14, 15. Western limits of *Pinus strobus* and *Liriodendron tulipifera*, species common in the northern deciduous forest formation. Stations beyond the general boundaries mostly occur on cliffs, in ravines or in valleys. The tulip tree is usually local in its distribution west of central Ohio.

5. The distribution of precipitation in successive years varies more in the prairie than in the northern forested region, and is more like that of the southern forests. The accompanying polar charts show a small fraction of a set made for about 100 stations east of the Rockies, covering periods of

11 to 35 years. The " precipitation patterns " are difficult to evaluate mathematically since the most important issue is the succession of dry and wet periods and their length and intensity.
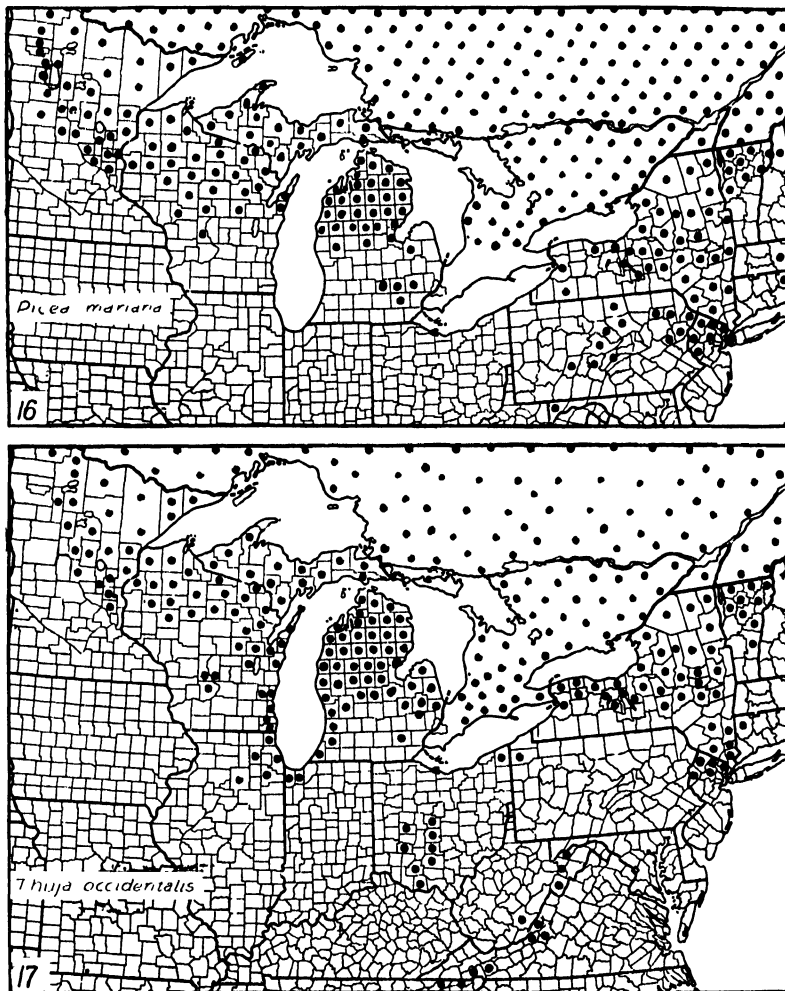


FIGS. 16, 17. Distribution of black spruce, *Picea mariana*, and arbor vitae, *Thuja occidentalis*, with outliers on cliffs and bogs, the former usually on acid, the latter on alkaline sites.

6. Precipitation is notably irregular in its areal distribution on the Prairie Peninsula. In 1930 the most intense drought followed the south margin of the prairie from the Ozarks through Kentucky to southern Ohio. In 1934 the most intense droughts were along the northern border. But throughout the five years there were areas like southwestern Ohio that suffered continu-

ously, and scattered areas in the Peninsula that experienced various alternate wet and dry seasons.

7. Prairie grass communities preceded prairyerths, but prairyerths once established favor the continuation of the prairie. There is now abundant
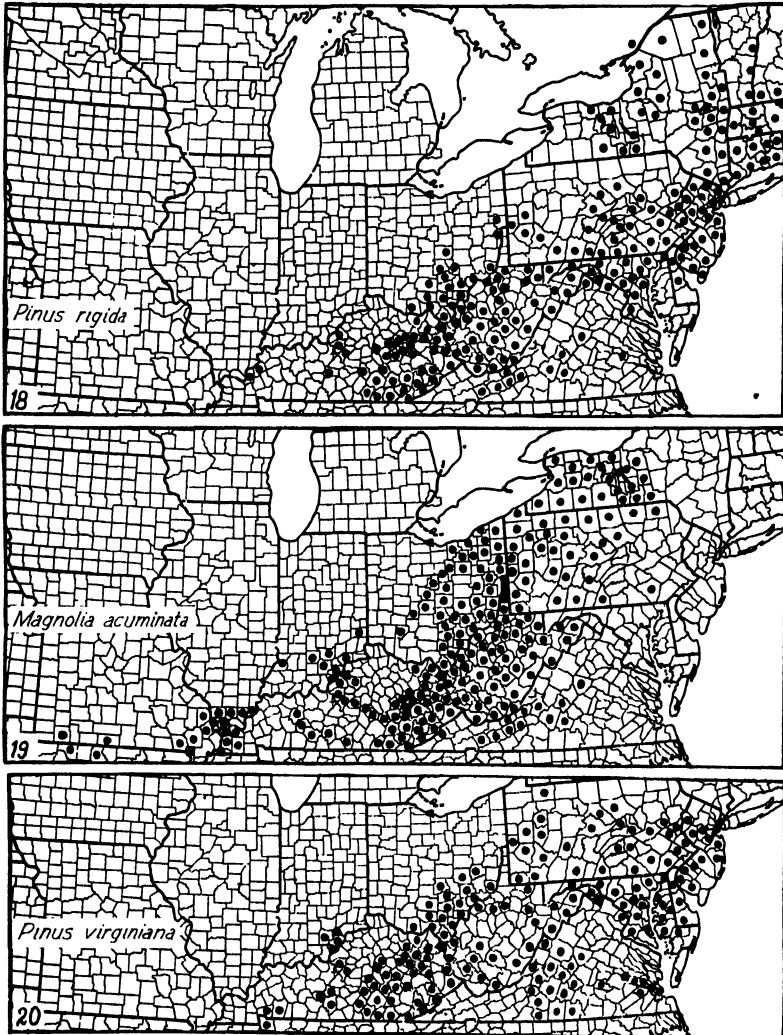


FIGS. 18–20. Distribution of two upland hard pines, *Pinus rigida* and *P. virginiana*, and of *Magnolia acuminata* of the deciduous forest formation showing the relation of their northern boundaries to the Prairie Peninsula.

evidence that the Peninsula was completely forested for a very long period of time before the present prairies came into existence.

8. "Mature" and "immature" soils may well define *local* tension lines

between different plant communities, but they cannot differentiate prairie and forest except in a prairie climate.

9. Tall prairie grasses once established exclude forest seedlings both by shading and, during the annual droughts, by superior utilization of available
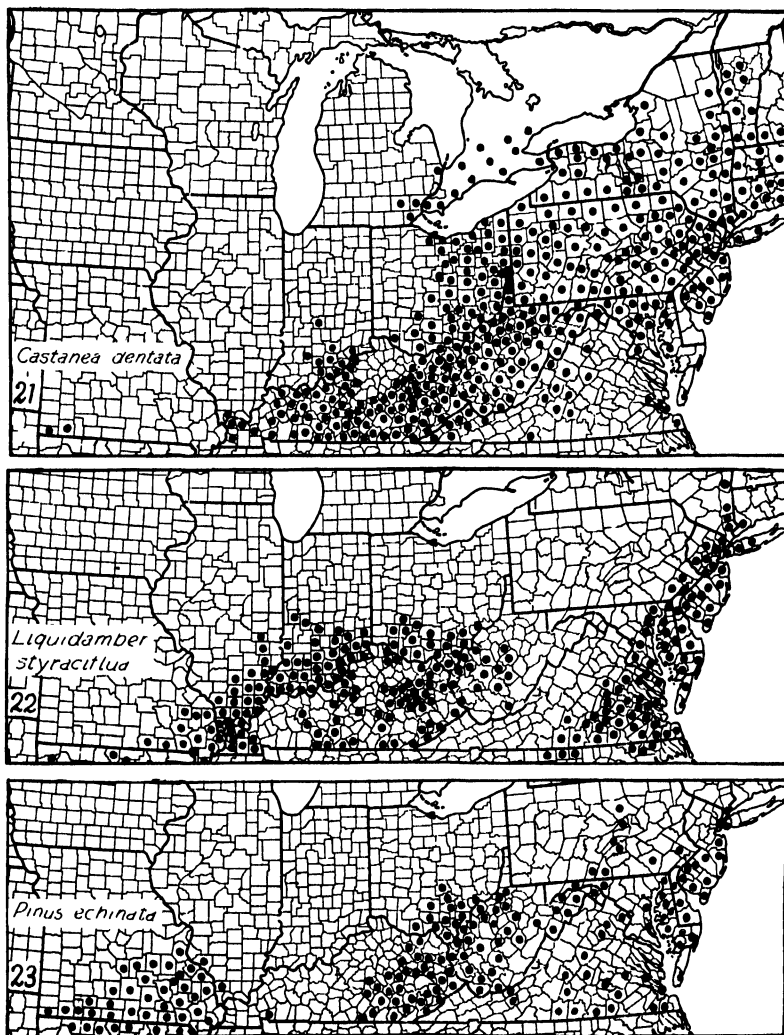


FIGS. 21–23. Distribution of an upland hard pine, *Pinus echinata*, and of two broad leaved species of the deciduous forest formation showing the relation of their northern boundaries to the Prairie Peninsula.

water in the deeper layers of the soil. On the more extensive prairies of Ohio the Andropogons formed a sod; on the many small outliers they grew as bunch grasses..

9. Fires favor the persistence of prairie species in contrast to tree species. Prairies preceded prairie fires. Whenever one searches the historical literature describing the period of settlement one is impressed by the frequent
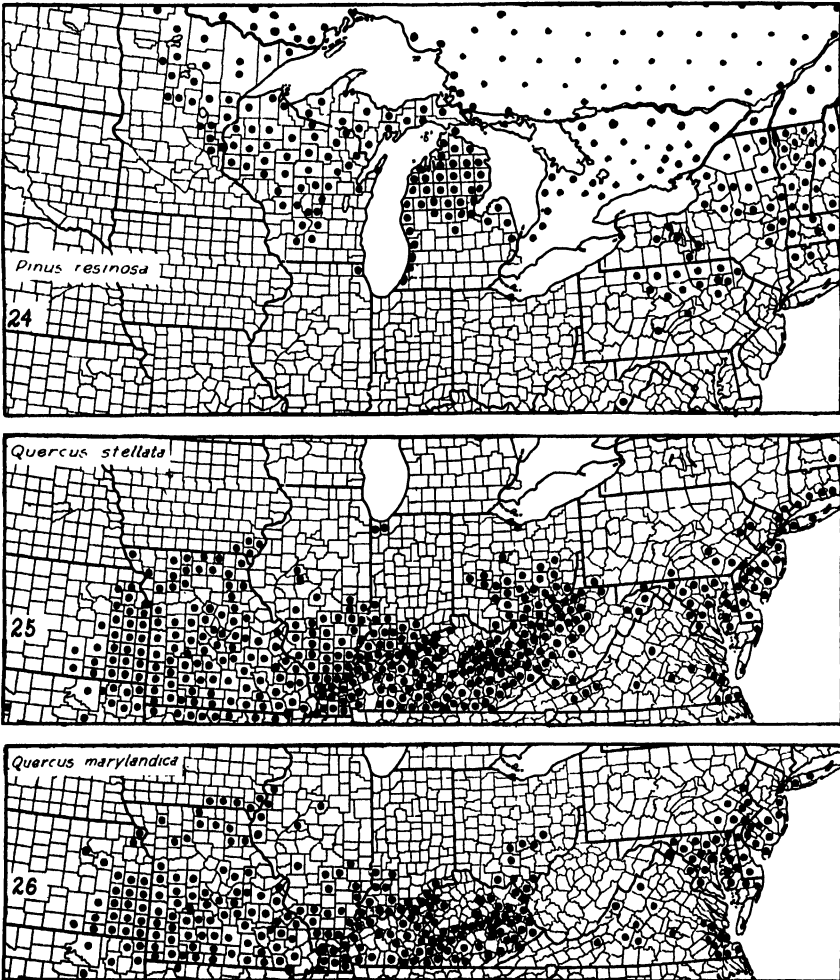


FIGS. 24–26. The boundary of the red pine, *Pinus resinosa*, has been pushed farther from the Prairie Peninsula than that of the white pine, and outliers are much less numerous. The post oak, *Quercus stellata*, and the black jack oak, *Q. marylandica*, have maintained themselves on the upland of the Peninsula, but are most numerous toward the drier west. Like *Pinus banksiana* to the north, these species have been eliminated eastward by competition with more mesophytic trees.

widespread fires usually ascribed to the Indians. Fire as an ecological factor, seems to boil down to this: that in forest climates it retards development, and may result in scrub, but it does not result in prairie. In a prairie climate it helps to maintain and perhaps rarely enlarges the prairie.

10. A late postglacial prehistoric dry period with more wide spread drought conditions and more prolonged droughts than at present is definitely indicated by certain bog pollen studies, by soil profiles, by the succession in bog profiles, by the absence, or rare occurrence, of many tree, shrub and herbaceous species from the region of the Peninsula, and by the present distribution of prairie colonies, and prairie species. The indication of a " Xeric Period " by bog pollen studies has recently been questioned. If pollen studies of the upper layers of peat within the Peninsular region fail to show a period of this kind either the methods of pollen analysis or the assumptions upon which they are based need further investigation.

11. Human occupation of the prairie region has modified both the prairie communities and the prairie environment. In the Peninsula the dry prairie knolls (as well as the forested uplands) became the home and village sites and
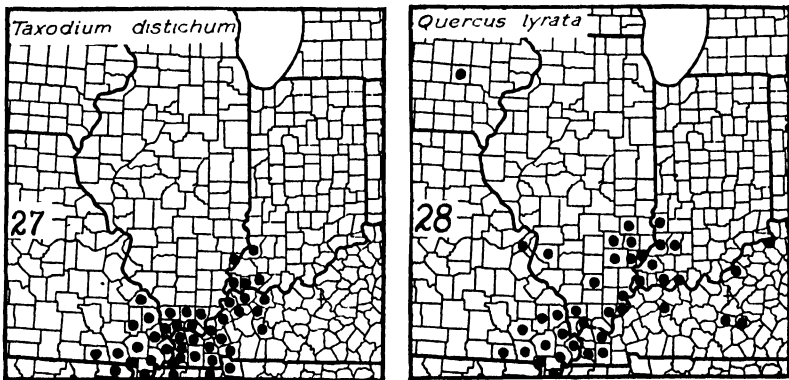



FIGS. 27, 28. The bald cypress, *Taxodium distichum*, and the overcup oak, *Quercus lyrata*, illustrate the geographic behavior of a number of species common in the Mississippi bottoms. They grow well when planted farther north, but are generally limited to the embayment. The Iowa record for the oak is a clump of trees antedating the time of settlement (Shimek).

their obliteration was completed many years ago. The wet prairies remained for a longer time, but the digging of thousands of miles of drainage ditches, and the laying of hundreds of thousands of miles of tile have long since completely altered the soil water relations. On most of the prairie farms from Illinois to Ohio the present (1930–1935) drought has led to the third general deepening of wells in order to secure an adequate water supply. At present in years of abundant rainfall the fraction that enters the soil in large part passes into tile drains and thence into ditches and rivers, and the ground-water table is only slightly or not at all raised. The present growth of trees on wet-prairie soil cannot be used as evidence that trees could have lived there a hundred years ago. Then during a part of nearly every year it was under water, and during another part it was desiccated, with cracks and fissures extending three feet or more into the subsoil.

12. One of the axioms of plant ecology is that the extremes of the factors are vastly more important than the means. As we may now witness, an extreme drought marked by lower precipitation, higher evaporation, higher temperatures and more intense light can change vegetation more in a few years than a century of favorable weather conditions. In Illinois thousands of oaks bordering the prairie died by the close of the 1913–1914 drought. In Ohio the present drought has killed or injured trees mainly on wet prairie or swamp forest sites.

13. It is quite useless to measure water content of soil at depths of six inches or even three feet if the data are to be used to explain differences in plant communities made up of species whose roots penetrate 8 to 10 feet.

14. It has become traditional to write that the Prairie Peninsula (and even the tall grass prairie as a whole) lies " in a forest climate, and therefore " etc. For example in Weaver and Clements' Plant Ecology we find on page 422 " Climates are to be recognized and delimited by means of their climaxes and not the reverse, etc." On page 424 " The causal relation is best shown when climate is taken into account but this leads to the difficulty found in the fact that the climaxes are themselves the best indicators of climate." On page 462 in discussing the " subclimax " prairie in contrast to the " true " prairie: " This community is necessarily regarded as an associes because of its *presence in a forest climate*, as well as by reason of the fact that shrubs and hardwoods are slowly invading it where the disturbance due to man is not too great." We can readily agree with the first two quotations, but the third needs far more evidence than has been presented up to the present time.

This point of view leaves out of account the idea of climatic equilibria and vegetation equilibria and their longtime shifts. There is not much to be gained by assuming that all of the " subclimax prairie " would be succeeded by forests " if present climatic conditions continue." The thing of which we can be surest is that it will not continue as it is. If these last few years are merely the beginning of a dry period, we should expect under natural conditions the prairie and the Prairie Peninsula to enlarge at the expense of the forest. If we are at the beginning of a period of increased rainfall, we should expect the forest to extend its margins perhaps greatly decreasing the " Peninsula "; but we should also expect the " subclimax prairie " to widen its area westward at the expense of " true prairie." In either case the prairie of the region from Iowa to Ohio seems to be just as " climax " and just as " true " as the other types of prairie farther west.*

* Since the above was written there has been received the annual report of Dr. F. E. Clements in the Carnegie Institution Yearbook No. 33. On page 193 he indicates that he is on the way to accept what the other prairie ecologists have known for 35 years: " that practically all of Iowa, southernmost Wisconsin and northwestern and central Illinois are to be assigned to the true prairie, a conclusion in closer accord with the rainfall-evaporation values." He then adds: " As a consequence, the *subclimax* or better *postclimax* tall-

15. Prehistoric factors are at least as important as present day measurable factors when dealing with the geographic phases of this problem. Until a time scale based on varves is established for the upper Mississippi region we cannot hope to date any of the climatic events that led to the development of the Prairie Peninsula, but there is sufficient evidence to estimate the duration at several thousand years.

Any proposed explanation emphasizing a single factor, or group of factors that does not take into account past climates, the soil types preceding the development of the prairyerths, and the vegetation types that antedated the Prairie Peninsula must fall far short of solving the complex of problems surrounding this unique ecological formation.

Finally, it must be said that in this limited space it has been quite impossible to cite the voluminous literature on this subject. The reader who knows the literature will have no difficulty in assigning credit (or discredit) for most of the ideas expressed. Many are older than " plant ecology " itself, some are new. The author has merely attempted a constructive critical inventory.

The accompanying distribution maps have been made possible thru the cooperation of more than thirty botanists who have sent me the county records for their respective regions. Most of the maps are incomplete but additional records will not greatly alter the boundaries discussed in this paper.

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grass prairie proper is restricted to the general vicinity of the margin of the deciduous forest, occurring likewise in extensive ' openings ' well .to the eastward." Since " the margin " is several thousand miles long this statement is beautifully noncommittal. It would be helpful also to know how, why, and to what, " subclimax " prairies became " postclimax " in 1934. Citation of the exact location of say three such "extensive ' openings ' well to the eastward " might explain all.

# ATMOMETERS OF POROUS PORCELAIN AND PAPER, THEIR USE IN PHYSIOLOGICAL ECOLOGY [1]

BURTON E. LIVINGSTON

## FOREWORD

This paper is dedicated to my life-long friend and colleague, Doctor Henry Chandler Cowles, whose thought and enthusiasm have exerted such notable influence in the rapid development of American ecology throughout a third of a century. His remarkable paper on sand-dune vegetation and his early appreciation of the dynamic relations of plant distribution to physiographic development came as enlightening encouragement to those who had dreamed that it might sometime be possible to approach problems of plant distribution from the physiological viewpoint. Studies like those of Cowles furnished a logical method by which the environmental complexes of plant habitats might be usefully characterized and classified according to soils and exposure, in terms of physiographic features that naturally pass through progressive changes with the lapse of years and centuries. Such simply descriptive terms as moraine, bluff, talus, bajada, beach, strand, lagoon, swamp, thus came to imply slowly changing systems of environmental conditions.

Of course the need for a still more penetrating examination of environmental complexes was realized. It was desirable that habitat features should be described in such terms as might represent conditions to which the individual plant is sensitive, which is not immediately true of geographic or physiographic concepts; at the same time, the terms of habitat description should be susceptible of physical and chemical measurement and integration whenever suitable techniques therefor might be developed. Accordingly, there has arisen a special branch of ecology, which has been called physiological ecology.

Considerable progress in physiological ecology had been made by agricultural chemists before ecology took its place among the biological sciences, and their studies on the soil relations of cultivated plants constituted an important part of the fundamental basis for the new science,—although it is still sometimes forgotten that ecology must logically include cultivated forms and weeds in its purview, as well as the components of natural plant associations and other natural vegetational units. Agronomy and horticulture furnish the most readily approachable fields for fundamental ecological research, and workers in these fields early turned their attention to soil characteristics as effective environmental features. It was soon realized that the soil condi-

tions that influence plants directly are mainly those of the soil solution, but that solution cannot even now be studied very satisfactorily, because suitable techniques therefor remain largely to be developed. These soil conditions are primarily temperature and the concentrations of the various soil solutes—ions and molecules, including water itself as well as oxygen and carbon dioxide.

Agricultural climatology also had contributed considerably toward the physiological aspect of plant distribution, especially with respect to air temperature and the more general considerations of precipitation, air humidity and sunlight (Livingston and Shreve, '21). The last two features are generally directly influential on plants while precipitation influences the water content of the soil, which, in turn, influences water supply and solute supply. Air conditions and radiation, as well as soil water content, influence soil temperature, which acts directly on plants.

With the possible exception of parasites and symbionts, competition and other biotic environmental conditions are generally indirect in their influence and they may be interpreted in terms of influential physico-chemical conditions, such as light intensity, soil-moisture conditions and the chemical make-up of the soil solution.

It appears that the first step in the logical analysis of environmental complexes should furnish us with a list of the conditions that we need to measure. Such a list might begin with physical conditions, including temperature of soil and air, soil moisture, precipitation, evaporativity and intensity of radiation (chiefly sunshine and skylight). It should then proceed to mention many chemical conditions, such as oxygen and carbon-dioxide concentrations or pressures in soil and air, and the concentrations of various kinds of influential solute ions and molecules in the soil solution—such as the cations of calcium, potassium, magnesium, iron, ammonium, hydrogen, sodium and the anions of nitrate, phosphate, sulphate, chlorine, the organic acids, etc. Kryptotrophic elements (such as boron and copper) may sometimes require attention. Really satisfactory comparisons between different habitats surely require the evaluation of such features, but only relatively small beginnings have thus far been made in that direction; just to mention the influential conditions that require measurement in any such comparison is difficult indeed, and most of them are not yet susceptible of satisfactory measurement.

From the standpoint of physiological ecology, any environment should be considered as a dynamic system (Livingston, '29, '34) that operates to supply materials and energy to organisms and to dispose of materials and energy that emanate from them. Therefore we need to envisage environments in terms of their supplying and disposing powers. Thus far, there have been a few attempts (see Wilson, '27, Wilson and Livingston, 32, Marshall, '31, Livingston and Koketsu, '20) to study natural soils in terms of their water-supplying powers, and the aerial environment is now rather commonly considered with respect to evaporativity. Temperature records for regions and

habitats abound, and temperature summations have been usefully employed by a number of ecologists, but the heat-supplying power of the aerial environment has not yet been much considered excepting in connection with a few studies in human ecology (see Hill, '19, Weeks, '30, '31), while the warming or cooling power of the soil remains to be suggested as an important dynamic environmental feature. The dynamic aspect of impinging illumination or radiation has been more or less indirectly appreciated in recent discussions, as in connection with photoperiodism, which is an important ecological feature. Still more useful criteria for natural light supply may become available later.

Having tentatively decided upon the directly influential environmental supplying powers that we wish to evaluate, our problem requires the invention of suitable instruments and techniques for the measurement of these things. For the most part, satisfactory instrumentation is still to be brought forward, but beginnings have been made with respect to precipitation, evaporativity, the water-supplying and oxygen-supplying powers of the soil, the carbon-dioxide-supplying power of the air, and perhaps some other dynamic features.

Because natural conditions are seldom constant in intensity for considerable periods of time, the evaluation of any environmental complex frequently involves the integration of each of its various effective components for whatever period is considered. Temperature summations of various types have been employed in the integration of air temperature and such summations may be secured by applying the planimeter to thermograph tracings. Some sort of heat integrator, following the principles illustrated in Hill's katathermometer (Hill, '19) and Weeks's " coolometer " (Weeks, '30, '31) would be very useful. Atmometers automatically integrate the value of evaporativity for the period of observation and the ordinary rain gauge, with a little oil in it, operates in a similar way. Although it is generally realized that records require integration, not much has been done as yet in this direction; indeed, the quantitative aspect of dynamic environmental relations has received comparatively little attention in ecology.

It should be noted that great precision of measurement and integration of environmental features is not yet required in physiological ecology; it is much more important that we first learn to measure conditions or habitat characteristics that influence plants directly (rather than those that influence conditions that influence plants, etc.). than it is that we hasten to develop extremely precise methods of instrumentation and computation. It should also be remarked that the ecological study of water-supplying power of the soil (which of course depends upon both precipitation and evaporativity) does not generally require knowledge of the exact values of this condition excepting when it falls below a critical range—perhaps about 80—100 grams per square meter per hour, for many ordinary plants (Livingston, '28). This consideration is based on the highly probable a priori supposition that plants are not directly influenced adversely by a supra-optimal water supply,

although adverse secondary or indirect influences that are themselves brought into action by a super-abundance of soil water may of course make it appear superficially that supra-optimal water supply is often injurious to many terrestrial forms.    Whenever the soil is obviously too wet for any plant the adverse influence of excessive water content is almost surely due mainly to unsuitable oxygen-supplying power, or H-ion-supplying power, or to unsuitable supplying powers of some constituents of the soil solution other than water itself.

The preceding paragraphs of this foreword represent in a mediocre way a very incomplete attempt to present a general and superficial picture of the sort of logical analysis that seems to be required as a basic foundation for the advance of physiological ecology.    It is clear that such considerations as these need to be thoroughly appreciated before we shall be able to devise instruments and techniques by means of which numerical indices of environmental capacity may be secured.    It is also clear that this sort of logical analysis must proceed hand in hand with the experimental development of instrumentation that seems to give promise of being helpful.    It is naturally impossible to fix upon the environmental components that we should try to measure unless we take into account feasible ways by which their measurement may be promisingly attempted.    Just what to measure must depend, to a considerable· extent and for a long time to come, on what we are able to measure.    Consequently, the most pressing present need for the further progress of this phase of ecology is the development of useful instrumentation and of the interpretation of instrumental results.    The methods of climatology and soil science are in many instances suggestive at least, but most of them still fail to furnish the sort of environmental indices that are required for studies in physiological ecology.

Environmental relations of plants and animals may be classified as subterranean or aerial, accordingly as the conditions dealt with are actually effective below the soil (or water) surface or above it (Livingston, '34).    Terminology based on Greek roots, for which the science of ecology has shown a remarkable preference in many instances, is so confused at present as to seem almost hopeless in this connection.    It seems best, therefore, if not for other reasons also, to employ common words wherever that is at all possible, trying to say simply just what we mean.    It is of course realized that solar radiation is aerial only in part; air conditions do act to alter the influx of radiant energy but the source of that energy is ultimately beyond the atmosphere, and the most influential fluctuations of radiation are causally related to astronomical conditions rather than to air conditions.    Also, evaporativity is not wholly an air condition.    The expressions " beneath the soil surface " and " above the soil surface " seem to be quite adequate here.    Employment of the words *edaphic* and *climatic* for this distinction would introduce difficulties of ambiguity with which most ecologists are familiar; for example, without special definitions *ad hoc,* one is never sure whether

soil temperature is to be considered as climatic or edaphic in nature, and *edaphic* seems sometimes to mean "local," and sometimes "effective within the soil."

The influential conditions comprising each of these two somewhat arbitrary but conveniently useful categories may be either restrictedly local or more or less extensively general; thus, for example, one may deal with aerial differences between the northerly and southerly exposures of a soil ridge only a few decimeters high, or with aerial differences between the eastern and western sides of a continent. In any case, however, it is the micro-climate rather than the macro-climate that actually influences organisms.

The environmental water condition that influences ordinary plants beneath the soil surface is, of course, simply the water-supplying power of the soil. The corresponding influence above the soil surface is evaporativity. This is a complex of air temperature, air humidity (water-vapor-pressure deficit), air movement and the intensity of impinging radiation. To a physiological ecologist one of the most attractive features of evaporativity lies in the fact that it can be usefully studied without any attempt to analyze it into its components. As far as water relations are concerned, physiological ecology must deal primarily with environmental indices or values to represent (a) the water-supplying power of the soil and (b) the drying influence (which is evaporativity) of the superterranean surroundings.

With a dawning appreciation of the general viewpoint that is partially outlined above, I was led, about thirty years ago, to begin a special study of the broader water relations of the individual plant and of distributional units such as societies, associations, consociations, or whatever they may be (Livingston and Shreve, '21). Possibly excepting the temperature or heat relations of organisms, their water relations are probably more generally influential in differentiating the physiological potentialities among different habitats than is any other group of environmental conditions. Also, environmental water conditions are most amenable to measurement and to useful integration.

Through a somewhat unusual concatenation of personal circumstances (notably through encouragement from such leaders as H. C. Cowles, F. K. Cameron, D. T. MacDougal, David Fairchild and Forrest Shreve; through the loyal cooperation of many students and visitors at the Johns Hopkins University; through financial support from the U. S. Department of Agriculture, from the Carnegie Institution of Washington, from the Pflanzenphysiologisches Institut at München and, in largest measure, from the Johns Hopkins University), I have been able to continue that study throughout these last three decades. Although not entirely neglectful of temperature and light conditions, nor of those environmental influences that are related to the mineral nutrition of plants, my attention has been continually devoted to plant water
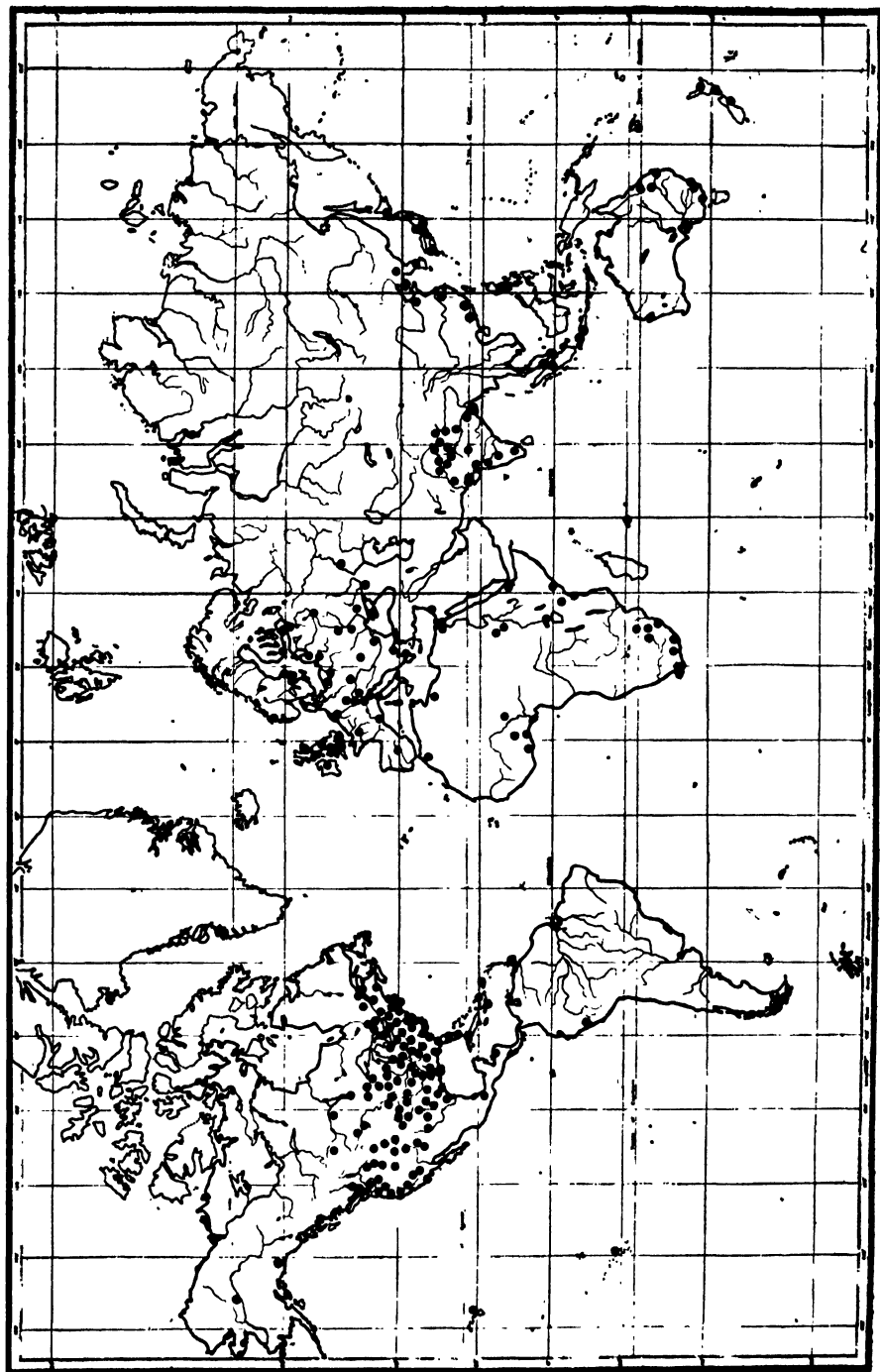
Fig. 1. World chart showing geographical distribution of porous-porcelain atmometers in last ten years.

relations. Throughout that period, many workers in this laboratory have had important parts in the advances that we have been able to make in this field. Hundreds of ecologists and experiment-station workers throughout the world have also had important parts, both independently and through finely cooperative personal correspondence with me, as well as through the ordinary channels of publication.

One of our main lines of study has dealt with instrumental means for the measurement of environmental evaporativity, especially with the characteristics and use of the Babinet type of porous-porcelain atmometer, which has come into such general use throughout the world since 1906 (Livingston, '06). The present paper is intended to show in outline the present status of our practical knowledge concerning that type of instrument. In recent years about a thousand standardized porous-porcelain pieces for atmometers have been sent out annually from this laboratory. The geographic distribution of localities to which they have been sent in the last decade is shown by the dots on the world chart of figure 1, but the scale of the chart is too small to permit all these localities to be indicated for some parts of the United States.

The following account of atmometers and their ecological use is in part a revision of mimeographed manuscripts prepared in December, 1931, and in March, 1935, and sent out to enquirers concerning these instruments. Early references may be found in papers published twenty or more years ago (Livingston, '10, '15), but many statements in those papers require correction or extension now. Because no fairly complete account of porous-porcelain atmometers and their use has been printed since 1915, because my correspondence files show that many hundreds of ecologists are deeply interested in these instruments, and because what progress we have been able to accomplish in the development of ecological atmometry represents the direct outgrowth of ideas and suggestions that first came to my mind from Henry Chandler Cowles at the turn of the century—for these reasons it seems appropriate to present this account here.

### EVAPORATIVITY, EVAPORATING POWER OF THE AIR AND EVAPORATION

The word *atmometer* applies to any instrument, of whatever form, for measuring or estimating different intensities of evaporativity, which is frequently called evaporation. *Evaporation* has at least two distinct meanings: (1) the influence of the environmental complex on the vaporization of water (which influence will be called *evaporativity* in this paper, following increasingly accepted usage) and (2) the process of water vaporization itself, usually at temperatures below boiling. *Evaporation* is sometimes used to denote also the quantity of water evaporated in a given time from some specified object; that is, " evaporational water loss." Evaporational loss divided by the length of the corresponding period of exposure is of course the mean evaporation rate for the period and surface considered. When the evapora-

tion process is negative it is *condensation*. The rate of evaporation from any given surface, for any period of time, is determined partly by (*a*) the characteristics of the liquid (or solid) water mass from which water vapor is being formed and partly by (*b*) the magnitude of the current evaporativity. Since evaporation is a surface process, its rate is influenced by conditions within the liquid (or solid) as well as by conditions that act from the gas-phase side. The influence of this latter complex of conditions (*i.e.* of the whole environment) constitutes *evaporativity*. These statements hold in general for all kinds of evaporation, but the present discussion refers only to evaporation of water.

The water-vapor pressure of a liquid (or solid) water surface, or its *vaporization pressure*, is the direct resultant of the internal conditions just mentioned. Its magnitude is determined by the temperature of the water and by the influence of non-aqueous materials dissolved or suspended in it or in contact with its surface. The corresponding actual vapor pressure of the gas phase immediately adjacent to the evaporating surface may be called the *condensation pressure*. The environment tends always to deposit liquid (or solid) water on the evaporating surface and the liquid (or solid) tends always to drive water vapor from the surface into the environment. When evaporation occurs vaporization pressure (internal) exceeds condensation pressure (environmental). When the evaporation rate is zero the two pressures are equal, and when condensation occurs condensation pressure is in excess. These statements apply just at the evaporating surface, on its two sides.

Although vaporization pressure is directly determined by conditions resident behind the evaporating surface (such as temperature, concentration of solutes, configuration of the surface) yet some of these conditions are indirectly more or less dependent, in turn, on the current environment; *e.g.*, air temperature. Evaporation itself tends to cool both the liquid and the adjacent air and condensation pressure is increased by the addition of the evaporated water vapor to the adjacent air.

Evaporativity embraces all the environmental influences that would tend to reduce retardation of evaporation or to accelerate that process if water were available to be evaporated from the standard surface. It needs to be emphasized that this environmental feature may exist at various intensities even in the absence of either liquid or solid water. It is the dynamic *capacity* or power of the surroundings to permit or to promote the evaporation of water, whether evaporation actually occurs or not. The magnitude or degree of evaporativity at any point in space is dependent (1) on the current water-vapor-pressure deficit in the gas phase adjacent to the point, (2) on the rate of renewal of the air in that region (air movement in any direction and at any rate; *wind* refers to air movement of considerable velocity, usually considered as nearly horizontal in direction), and (3) on the intensity of impinging radiation at the point (sunshine, sky radiation, earth radiation, etc.).

The water-vapor-pressure deficit is simply the difference between (a) the water-vapor pressure of the water at the evaporating surface, at its current temperature and with the current barometric pressure, and (b) the actual partial pressure of water vapor in the neighboring air. The *evaporating power of the air* represents that portion of current evaporativity which is not directly related to radiation. It thus embraces current air temperature, current water-vapor-pressure deficit and air movement. It is really the capacity of the environment to receive water vapor from some standard evaporating surface. (The rate of evaporation from a specified surface would of course be greater if there were no gas present in the adjacent space.) This expression, evaporating power of the air, may be synonymous with evaporativity when radiation influence is regarded as negligible.

*Vapor-pressure deficit* should replace *relative humidity* in all studies concerned with the *dynamic drying influence* of the environment; that is, whenever rates of evaporation and transpiration are being considered. It takes account of both air humidity and air temperature. Relative humidity is not constantly related to vapor-pressure deficit excepting when air·temperature is constant. Thus, two psychrometric or dew-point observations may give the same value of relative humidity with different air temperatures, but the dynamic drying influence of vapor-pressure deficit is greater as air temperature is higher. For example, suppose air and water temperature to be 20° C. at one observation and 30° C. at another, and that relative humidity is 60 per cent. in both cases; for the first observation the vapor-pressure deficit is 7.0 mm. (of mercury column) and for the second it is 12.6 mm.; therefore evaporation from a specified water surface should proceed much more rapidly in the first case than in the second, when the combined influence of air movement and radiation is the same for both observations. The general relation between vapor-pressure deficit (D) and relative-humidity percentage (H) is shown by the following equations, in which V is the vapor tension of liquid water at current water temperature and P is the actual partial pressure of water vapor in the adjacent air :—

$$D = V - P; H = 100 \, P/V.$$

Assuming water and air to have the same temperature, some approximate data for pure water are shown by the following tabulation.

| | Temperature | V | P | D | H |
|---|---|---|---|---|---|
| 1st case | 20° C. | 17.4 mm. | 10.4 mm. | 7.0 mm. | 60. p.c. |
| 2d case | 30° C. | 31.6 mm. | 19.0 mm. | 12.6 mm. | 60 p.c. |
| 3d case | 30° C. | 31.6 mm. | 24.6 mm. | 7.0 mm. | 78 p.c. |

It is interesting to note that to reduce the deficit value (D) for the second case (12.6 mm.) to that shown for the first case (7.0 mm.), without altering

the higher temperature (30° C.), would necessitate a relative humidity (H) of 78 per cent. instead of 60 per cent., and an actual vapor pressure (P) of 24.6 mm. instead of 19.0 mm.

Such considerations as these are fundamental to clear analyses of environmental influence on organisms and they surely deserve more attention than they usually receive.·

When *static* conditions only are to be considered (as when, for example, the air humidity of a chamber is to be maintained so as to be in moisture equilibrium with pieces of wood or paper of specified moisture content), then air humidity is of course to be reckoned in terms of relative-humidity percentage rather than in terms of vapor-pressure deficit. For instance, air-dry paper at the temperature of the surrounding air should maintain a constant moisture content in an atmosphere of the proper maintained relative humidity, even when temperature fluctuates. Thus, the concept of relative humidity is useful in some kinds of study, although its employment as a measure of the influence of air moisture on evaporation, transpiration and human comfort is always misleading unless all of its values to be compared refer to the same air temperature.

Evaporativity may be studied in rooms, greenhouses, culture chambers, etc., as well as out of doors for various kinds of exposure—as in the open, in the shade of trees or screens, near the ground or at greater heights, etc. It is one of the most important of the complex environmental features that influence plant, animal and human life. Its magnitude in nature usually fluctuates, with more or less regular hourly, daily and seasonal march. It varies from location to location for the same instant, and different locations generally exhibit different kinds of fluctuation for the same period of time. Because of its fluctuation, the magnitude of evaporativity is usually expressed as a mean or a total for a given time period, which may be indefinitely short or may be as long as an hour, a day, a month or a year. Although it should ideally refer to just a point in space, it really always must necessarily refer to some standard evaporating surface, the characteristics of which are supposed to be always effectively the same, excepting as they are influenced by the components of evaporativity itself and by the rate of evaporation. Its measure for any period is the amount of water evaporated from the standard surface in that period and for the specified exposure. Units of evaporativity are consequently weight or volume units showing rates of evaporational water loss from the atmometer employed. Volume units (as milliliters per hour or per day) are often used for convenience, instead of the more precise weight units (as grams per hour, etc.). When the standard surface is that of free liquid water or aqueous solution in an open pan or tank, linear units of depth are sometimes employed (as centimeters of depth lost from a standard tank per day, etc.). Weight or volume measures may of course be computed from depth measures for plane surfaces.

Many attempts have been made to calculate numerical indices of evapora-

tivity from measurements of water and air temperature, air humidity, wind and radiation intensity, but the labor thus involved is much greater and the results thus obtained are much less satisfactory than when readings are made directly from a standard atmometer. We simply measure evaporational water loss from a standard instrument, express this as an average time rate and employ that rate as our measure of the capacity of the surroundings to receive water vapor from the specified surface for the period considered. All comparable values must refer to the same instrument or to instruments that are very closely similar. It is entirely beyond the realm of practical possibility to bring readings from different kinds or sizes of atmometers into a homogeneous series unless the internal differences among the several instruments are effectively very slight indeed. Sufficiently slight differences may be practically cared for by calibration, however. It follows that every series of evaporativity data must be accompanied by specification of the sort of atmometer from which the values were derived and to which they are to be referred. Only in a very general and superficial manner can comparison be made between evaporation rates from different types of instruments. This is not always appreciated. If two atmometers of different type are exposed to the same conditions of air and radiation for the same period, their rates of evaporation generally differ not only with respect to the areas of the evaporating surfaces (to which the rates are *not generally proportional*) but also with respect to the shapes of the instruments and to the amounts and arrangements of the materials of which the instruments are composed, including the contained water.

Different types of atmometers have been devised for different kinds of studies but it is supposed in all cases that the internal characteristics of any type are adequate for the maximal evaporativity intensities dealt with, that they are maintained throughout the period considered and that all instruments used for precise comparisons are effectively alike in all respects. If the instruments used differ but little or if any instrument alters slightly but significantly with use, then differences and alterations are to be cared for by means of correction coefficients derived from calibrations or standardizations instituted from time to time.

It is very essential that the water-vapor pressure of the standard evaporating surface shall be maintained, excepting as it fluctuates with temperature. When a porous body (such as cloth, paper, porous porcelain) furnishes the evaporating surface, the peripheral part must not become significantly drier, even with the most intense evaporativity dealt with. Whenever the environment is capable of removing water from the instrument faster than water is supplied at the evaporating surface, the rate of supply limits the rate of evaporation, which is then a measure of the supplying power of the instrument rather than of environmental evaporativity. An atmometer sphere of material that is too dense or not adequately porous (for example, an ordinary sphere that has been seriously clogged by salts in the pores) may, on a typical day,

perform satisfactorily only during the early forenoon and late afternoon hours, but the rate of evaporation may be maintained practically throughout the mid-day hours. In such a case, a time graph of the march of evaporational water loss ascends to its maximal ordinate value, continues horizontal throughout the mid-day period and then descends. The plateau, or horizontal portion, of such a graph shows nothing about the corresponding intensities of evaporativity excepting that they continuously equalled or surpassed the maximal ordinate value. If the dynamic water-supplying power of a porcelain sphere is very low the rate of evaporation therefrom may remain constant throughout the entire 24-hour period. This consideration probably explains how one eminent experimenter with porcelain atmometers was able to report that he once had one of them that he dubbed " his standard instrument " because it always lost water at a constant rate, without any relation to environmental changes. While engaged, at this laboratory, in studies on the Askenasy demonstration of truly negative tension in liquid water, Grace Lubin (now Mrs. J. E. Finesinger) severely clogged the pores of a porous-porcelain sphere by externally applying a very dilute " solution " of Para rubber in benzene and allowing the benzene to evaporate, after which the sphere was mounted as an atmometer and read daily for a number of days; it lost almost exactly 1 ml. of water each day, whether the intensity of evaporativity were high or low: The pores of this sphere had been very markedly clogged with rubber, but the instrument was not quite waterproof. Those familiar with the principles involved in the effectiveness of superficial mulches to retard evaporation of water from soil will note that the clogged sphere performed somewhat as a mulched soil; the periphery was constantly so dry that its water-vapor pressure was inadequate even for the lowest intensities of evaporativity experienced.

The general principles thus far briefly outlined may be applied satisfactorily for a considerable degree of precision in atmometric readings, but the nature of many evaporativity studies requires no more than a low degree of precision and an investigator must decide to what extent he will attend to having all his readings refer to the supposedly standard surface. In general, ecologists have perhaps not been as careful in this connection as might be desired, but meticulous care is to be avoided unless it is really warranted by the nature of the problem in hand.

## TYPES OF ATMOMETERS

*Open Pans.*—The simplest form of atmometer is an open pan of liquid water, practically pure. Losses are measured from time to time (in terms of depth, weight or volume) and the water level is approximately maintained by frequent replenishing. The shape, size, material and color of the container are highly important characteristics. The evaporating surface is of course horizontal and exposed upward, except for fluctuating alterations due to ripples and waves. Upward projection of the pan wall above the water

level is not desirable but cannot be wholly avoided. Wind tends to cause occasional splashing over if this projection is small. Through the formation of ripples and waves, wind increases the extent of the evaporating surface and causes its shape to fluctuate to an uncertain and variable extent. Rain and dew add water to the pan and rain may cause splashing. Animals are apt to remove water from the pan; insects such as moths may be trapped in the pan and their floating bodies may alter very significantly the nature of the evaporating surface. Ordinary water (not distilled) is commonly used but an aqueous solution may be used to avoid ice formation in freezing weather (Livingston and Haasis, '29). Open pans are generally suitable only for the very roughest sort of climatic measurements when an upwardly-directed horizontal evaporating surface is desired. For different kinds of studies pans of different sizes, shapes and materials have been employed, but all pans of any series must be alike to give homogeneous data.

Open pans may be weighed from time to time. Volume readings may be computed from depth measurements, which are generally used directly when the pans are not weighed. Several forms of depth gauge have been employed for measuring the depth of water in the pan. At frequent intervals water is added, the pan being filled to the original depth or to the original weight. The volume or weight of water needed at each refilling may of course be used as the reading.

*Wet paper or cloth.*—To avoid some difficulties and inconveniences incident to the use of open pans, many forms of atmometers with paper or cloth evaporating surfaces have been described (Livingston, '10, '11, '15). The porous material is kept wet automatically by means of a distilled-water supply from a reservoir and readings are secured in terms of weight or volume. The best-known forms of this type are the atmometers of Piche (1872) and Cantoni (1879), which expose small disks or circles of thick filter paper or blotting paper, permitting evaporation from the cylindrical edge of the circle as well as from its two plane surfaces, except for a small area in the center of each, where the water supply is introduced. The circles may be horizontal or may have any oblique angle. They cannot be cleaned and are consequently to be renewed from time to time. The diameter of the paper circle used is limited by the highest evaporation rates that are to be measured; if it is too large the marginal portion becomes drier when evaporativity is intense, which virtually amounts to a reduction of the evaporating surface. With the original forms of mounting, maintenance of adequate connection with the water reservoir is apt to be practically somewhat difficult. In the arrangement employed by Piche the paper circle is pressed upward, at its center, against the lower, otherwise open, end of a vertical graduated glass tube that is closed above and serves as reservoir. Pressure is applied by means of a suitably supported disk of sheet metal below the paper circle and slightly larger than the end of the tube. Air is best admitted, replacing the water lost by evaporation, through a pin-hole at the center of the circle. In the arrangement used

by Cantoni the paper circle is pressed downward against the upper, otherwise open, end of a tube leading from a reservoir at a lower level. A hard-rubber mounting for paper circles, suitable for use with burette or bottle reservoir at a lower level, which has been developed in this laboratory, will be referred to later on. Wet paper circles are more responsive to wind fluctuations than any other form of atmometer in general use. Unless very nearly horizontal, however, (or unless carried on a suitable rotating table or clinostat, with vertical axis) they are necessarily exposed unequally to wind from different points of the compass. Paper and cloth are not suitable for use in freezing weather.

*Porous-porcelain pieces.*—In 1813, in some of his historically important studies on evaporativity, Sir John Leslie used a hollow porous-porcelain sphere attached to the lower end of a calibrated glass tube that was open above and served as reservoir. Such an arrangement exudes liquid water, forming a film or drops on the outer surface of the sphere, if evaporation is slower than the rate at which the existing water column causes liquid water to pass outward through the porous walls. To avoid exudation of liquid when evaporation is slow, the permeability of the porcelain must be relatively small, but then the evaporating surface may become too dry when evaporation is intense. Consequently the internal characteristics of this device may alter with changes in environmental evaporativity.

Babinet (1848), Marié-Davy (1869), Mitscherlich ('04) and Livingston ('06, '08) all devised the now common type of porous-porcelain instrument independently. Babinet, Livingston, and Transeau ('10) employed vertical hollow white cylinders, like filter candles or bougies, open below but closed and rounded above. Mitscherlich's porous-porcelain cylinder was itself open at both ends but the upper end was closed by a cemented plate of glass. In all these instruments exposure is alike toward all points of the compass; slight deviation from the vertical position does not generally introduce significant difficulties with regard to wind direction. The relation of cylinders to radiation will be considered below.

In these instruments the cylinder is filled with distilled water, which is continuous, through a rubber stopper and tube, with a reservoir at a lower level, and atmospheric pressure on the water in the reservoir keeps the tube and cylinder cavity filled while evaporation from the external porcelain surface proceeds much as in Cantoni's paper instrument. Thus is avoided the possibility of exuded liquid appearing on the outer surface of the porous porcelain. The hydrostatic pressure within the cylinder is always *positive*, but somewhat less than the current barometric pressure. (Some writers are accustomed to introduce possible confusion of thought by calling a hydrostatic pressure *negative* when it is greater than zero but less than current atmospheric pressure, but of course a truly negative pressure should be less than zero—liquid under negative pressure being actually somewhat stretched.) The external pore openings of the porcelain wall are effectively closed against air entrance (excepting dissolved air) by the tiny water-air menisci formed

across the openings. These menisci are of course held in place by adhesion of water to porcelain and by water cohesion (capillarity and surface tension). Livingston's white porous-porcelain pieces require when wet several atmospheres of air-pressure excess to force out the liquid plugs and drive air through the wall. Evaporation occurs from the outer surface of the cylinder and liquid water moves up from the reservoir below and out through the porous walls at a rate just adequate to keep the instrument filled and to maintain the microscopic menisci at the external pore openings. Readings are secured from time to time, either by weighing the instrument (the more precise method) or by volumetric measurement of the amount of water lost from the reservoir during the preceding observation period. Only distilled water may be used. Rain and dew are absorbed by these instruments unless the mounting is arranged to prevent such absorption.

All forms of porous-porcelain atmometers now in use are constructed on these principles. Modifications of the original instruments of Babinet, Mitscherlich and Livingston have involved only the shape of the porous-porcelain member, its porosity, its color and the arrangements of the mounting. White spheres (Livingston, '15, Livingston and Thone, '20) are now generally used; they are about 5 cm. in diameter, with a small cylindrical neck below, to which the supply tube is attached by means of a rubber stopper. Flat circular plates of porous porcelain were first employed in this way by Bellani in 1820, long before Babinet's announcement in 1848, but they have never been generally adopted. It is notable that Bellani was apparently the first to employ the principles of the porous-porcelain atmometer with reservoir below, and that Cantoni's similar arrangement of a paper circle was not described until 1877. The present general use of porous-porcelain atmometers by students of ecology and physiology has developed since the publication of Livingston's first description of his cylinders in 1906. His modification of Bellani's plate was announced in 1915. Spherical porous-porcelain pieces have been increasingly used throughout the ecological world since that time (Livingston, '15; Livingston and Haasis, '29, Chalkley and Livingston, '29).

Although properly exposed for wind influence on evaporation, vertical cylinders do not receive solar radiation always at the same angle. This particular defect may be corrected by giving the cylinder a suitable slant upward toward the north and altering the slant from day to day or from week to week, as the season changes; but a slanting stationary cylinder is not properly exposed for wind influence. All horizontal plane surfaces (pans, paper circles, Bellani plates) are properly exposed for wind effect, but solar radiation impinges on them at an angle which varies throughout the day and differently for different seasons. A Bellani plate or a Cantoni paper circle may be · mounted on a suitable heliostat arrangement and thus properly exposed to sunshine at all times, but such an arrangement necessarily gives an improper exposure to wind. The influence of solar radiation on evaporation from a blackened Bellani plate is at its maximum when the plate is perpendicular to

the direction of the impinging rays, but this influence is significantly less when effective rays meet the plate at an angle of somewhat less than 30° from the perpendicular and it rapidly becomes still smaller as the angle increases beyond 30°. A spherical evaporating surface is the only one that gives proper exposure to both wind and radiation at all times.

Still other types of atmometers have been devised and described from time to time. Several of these employ cloth or paper for the evaporating surface, with ingenious methods of mounting. Open pans of soil or of some standardized mineral powder have been used in many studies. Open pans of aqueous solution—as of glycerin or some other very soluble and non-volatile substance—are used instead of water pans in freezing weather (Livingston and Haasis, '29). Excepting for studies with special requirements, the most useful forms are open pans, porcelain cylinders or porcelain spheres. The porous-porcelain sphere is generally best for ecologoical and physiological study, especially when radiation effects are to be included in the evaporativity integration.

## Atmometer Records

Atmometric records are primarily simply increments of evaporational water loss from the standard evaporating surface used as atmometer. For each observation interval the reading represents the amount of water actually lost through evaporation under the influence of the current environmental complex. Intervals may be of any convenient and suitable length and several readings for short intervals may be summed to give a reading for a longer period. Mean rates may be computed as per minute, per hour, per day, per week, per month, per season, etc. When short-period fluctuations are to be studied it is necessary that observation intervals be relatively short, or else some suitable form of automatic recorder is to be employed.

Several recorders have been devised and used by various workers. Sometimes a recording balance is used and sometimes the descent of a float in the reservoir is traced on a clock-driven drum. These appliances are to be specially constructed according to the needs of the user. An interesting type of recorder, first described by Chalkley and Livingston ('29), operated by automatically tracing a time graph of the hydrostatic-pressure fluctuation within the atmometer tube when entrance of water from·reservoir to tube was at all times retarded by means of a standard permeable resistance member. The resistance used was a small conical porous-porcelain cup (a Livingston " soil-point cone ") and a large-bore U-tube of mercury acted as manometer. A float on the outer mercury meniscus rose when the internal hydrostatic pressure decreased (with slowing down of evaporation) and fell when the pressure increased, and this float actuated a pen which descended when the float rose, and conversely. The pen traced a record on a paper strip borne by a vertical clock-driven drum. Ordinates of the resulting graph were taken to represent instantaneous rates of evaporation, on the supposition that the

rate of evaporational water loss from the instrument (equivalent to the rate of water movement upward through the standard resistance member) ought to be proportional to the internal hydrostatic pressure, to which upward movement of water is due. This supposition is not tenable, however, unless the water temperature in and adjacent to the fine-pored resistance porcelain is maintained constant, as was pointed out in an excellent discussion by Christiansen, Veihmeyer and Givan ('30); for, since the viscosity of water increases with decreasing temperature, the relation between rate of flow through a constant resistance and the driving head of hydrostatic pressure fluctuates considerably with temperature within the ordinary climatic range of the latter. This difficulty may be overcome by maintaining a nearly constant temperature in the water of the reservoir in the vicinity of the resistance member, or the changing temperature of the water may be recorded by means of a suitably installed thermograph and the evaporation tracing may be subsequently corrected for temperature changes in the resistance member. This influence of temperature on the viscosity of water will be reverted to below, in connection with the instantaneous reading atmometer.

As usually operated, atmometers are self-integrating instruments and the reading for an observation interval represents an integration of all the fluctuating influences that have been effective in the interval. Atmometer readings are measures of the time rate of the accomplishment of work; namely, the work of vaporizing and removing water from the standard evaporating surface used. Since the evaporating surface is supposed to be maintained in all essential respects throughout the period of operation, the readings are measures of the capacity of the environmental complex to permit or to further evaporation from the particular surface employed.

## ATMOMETRIC UNITS

When open pans are used as atmometers, for comparatively superficial and rough estimates, depth units are employed by many observers. The centimeter is in common use but some government institutions and some individuals use the inch. Depth of evaporation from a standard atmometer pan is not measured with any high degree of precision, and observational errors of depth readings are naturally augmented by corresponding errors introduced when the pan is replenished, which must occur at short intervals to avoid introducing an additional instrumental error due to significant fluctuation in the water level.

Weight units are properly used for all types of atmometers. A recording balance may be employed to secure automatic records of weight decrease. With cloth, paper and porcelain instruments, volumetric units are commonly used—generally milliliters (cubic centimeters). The reservoir may be a bottle, a graduated cylinder or a burette, etc. Errors are of course introduced by thermometer effects within the instrument when volumetric readings

are not all taken at the same water temperature but these are negligible in most ecological and physiological studies.

Whatever units are used, each reading or record should generally refer to: (1) the sort of instrument used, (2) the beginning and end of the observation interval considered, (3) the time unit in terms of which the mean time rate is computed, (4) the geographical location of the observation station, (5) the height of the instrument above the ground and (6) the exposure with reference to wind and radiation. One might write, for example, that (1) a standardized white porous-porcelain sphere, 5 cm. in diameter, operating (2) from 6 A.M. to 6 P.M. on July 12, 1929, lost water (3) at the mean rate of 1.5 ml. per hour, the instrument being (4) near the village X, (5) 10 cm. above the ground and (6) among clumps of tall grasses.

Excepting for special studies on relations between area, shape, etc., of the standard evaporating surface, readings are not to be computed in terms of the area of the surface used, for such computation is usually quite useless and is apt to be misleading. Specification of the sort of instrument employed implies adequate information concerning the extent and form of the evaporating surface. It must not be forgotten that rate of water loss per unit of area varies for different types of instrument as well as with the intensity of environmental evaporativity, and that readings of different instruments cannot be homologized unless the instruments are very nearly alike with respect to all effective characteristics.

### Types of Standardized Porcelain Pieces

Three forms of white porous-porcelain pieces are now in general use for atmometers: cylinders, spheres and Bellani plates. The cylinders (Livingston, '06, '08, '10, '15) (fig. 2, a) are about 3 cm. in outside diameter and 13 cm. high, the top closed and rounded, the bottom open. The open end, with internal diameter about 2.5 cm., is strengthened by a double-thickness rim about 2 cm. high. The smooth-ground outer surface is water-proofed for a distance of 5 cm. from the lower end, the uncoated part being 8 cm. high. In operation the cylinder is mounted on the upper end of its supply tube, by means of a one-hole rubber stopper, being generally placed vertically with the closed end above. Thus mounted, cylinders integrate the effects of water-vapor-pressure deficit of the surrounding air and those of wind from any horizontal direction, but the vertical position introduces troublesome inequalities of exposure to radiation from sun and sky, as has been noted.

Since white spheres became available (Livingston, '15, '15c) the use of cylinders in atmometry has been generally abandoned excepting for beginners' demonstrations and some kinds of forestry studies. The white sphere (fig. 2, b) is about 5 cm. in external diameter, with cylindrical neck 4.5 cm. long and 1.9 cm. in external diameter. The outer surface is smooth-ground and the neck is water-proofed outside. The supply tube is attached by means of a rubber stopper in the neck opening. Mounted with neck vertical, the

sphere is satisfactorily exposed to air temperature, air moisture, air movement and impinging radiation, for the spherical surface is large in proportion to the diameter of the neck and thus the irregularity of form due to the neck may be neglected.
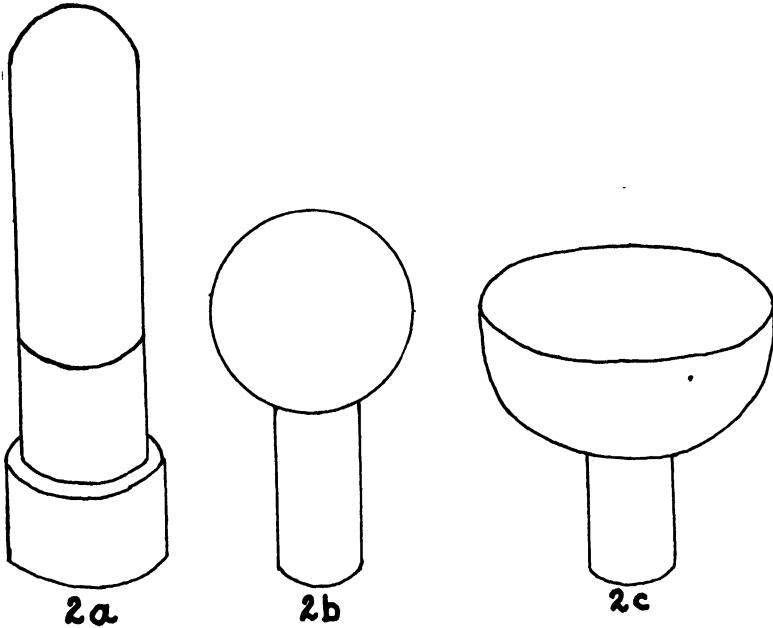


Fig. 2. Porous-porcelain pieces: 2a, original type of cylinder; 2b, sphere (white or black); 2c, Bellani plate.

Bellani plates (fig. 2, c) are plane circles 7.5 cm. in diameter, closing the large end of a funnel-like base, which is nearly hemispherical and has a cylindrical neck 4 cm. high and 2 cm. in outside diameter. All but the plane surface is waterproofed. The supply tube is attached as in the case of the sphere. Mounted with the circular plane surface above and horizontal, these pieces are satisfactorily exposed to air temperature, air moisture and air movement, also to the *vertical component* of impinging radiation from sun and sky.

The wall thickness of all porous-porcelain pieces is about 3 mm. Each standardized piece bears on the water-proofed part of its surface a serial number for identification (such as 35—705), and also its coefficient of correction (as 0.78).

Blackened spheres are white spheres with a film of collodion and washed lampblack (Livingston and Wilson, '26) completely covering the spherical part. The collodion film is ripened under water and must never be allowed to dry. When not in use these spheres are kept under water or else wrapped in wet filter paper and enclosed in suitable jars. Some formaldehyde added

to the water used for storage hinders the development of fungi. White spheres may be blackened by painting with thoroughly washed lampblack (Livingston, '23) in distilled water, but the coating thus produced is easily injured. Since black spheres have been obtainable the use of blackened ones has been largely discontinued.

Black spheres have been available since 1932. In the preceding 20-year period many attempts to secure these from pottery makers in Germany, England and the United States had been made from time to time, but these had been unsuccessful. The new pieces, which are very satisfactory indeed, are now made in this country. The black sphere resembles the white one in all respects excepting that it is composed of black porous porcelain, which is slightly more fragile than the material of the white pieces. The water-proofed neck of the black sphere is coated with a white lacquer.

When mounted with its neck vertical, the black sphere has the same exposure to all evaporativity components as the white sphere has when similarly mounted and it performs in the same way, excepting that the white sphere absorbs but little of the impinging radiation from sun, sky and earth, while the black sphere absorbs these radiations much more completely.

## Some Mountings for Porcelain Atmometers and Their Installation

The mounting for any porous-porcelain piece consists essentially of supply tube and reservoir. The supply tube, which serves to support the porcelain piece as well as to supply water, is usually of thick-walled glass tubing with bore of about 6 mm., but tubing of hard rubber, brass, copper or block tin serves well. This tube carries near its upper end a one-hole rubber stopper that fits the porcelain piece tightly when about half of the stopper projects (as finger hold). Various types of mounting have been employed.

A simple style of mounting (fig. 3) has a straight supply tube of glass, about 30 cm. long, with internal diameter of about 6 mm., held upright in a narrow-mouth half-liter or liter bottle by means of a tightly fitting, drilled, preferably cylindrical ("straight") cork stopper. The lower end of the tube reaches nearly to the bottom of the bottle when the cork is in place. Neither length of tube nor level of water in the reservoir bottle exerts any notable influence on the rate of evaporation from the porcelain piece above. Since entrance of air into the bottle is necessary, as water is withdrawn, the cork bears, in a second perforation, an air-vent tube (of soft copper, brass, hard rubber or glass, with outside diameter about 3 mm.) having the form of an inverted J whose longer arm reaches downward only to the lower surface of the cork. This tube may be replaced by a diagonal groove cut in the side of the cork if the instrument is not to be exposed to rain. When tightly set, the cork should project above the bottle neck sufficiently to furnish a firm finger hold. Somewhat above the base of the bottle neck is
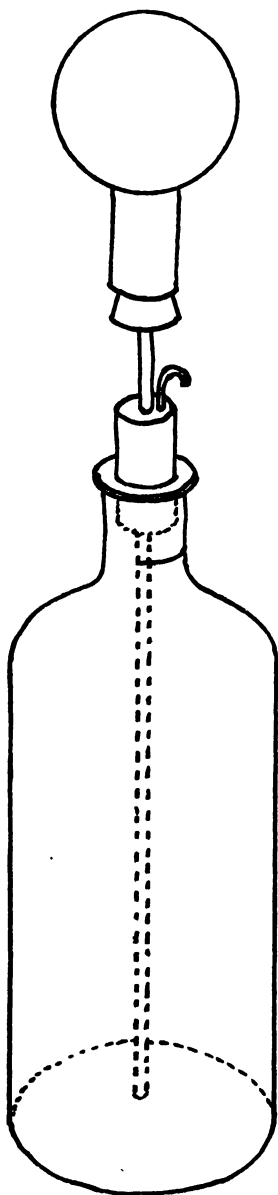
FIG. 3.　　　　　　　　　　FIG. 4.

FIG. 3. Simple mounting for porcelain atmometers.
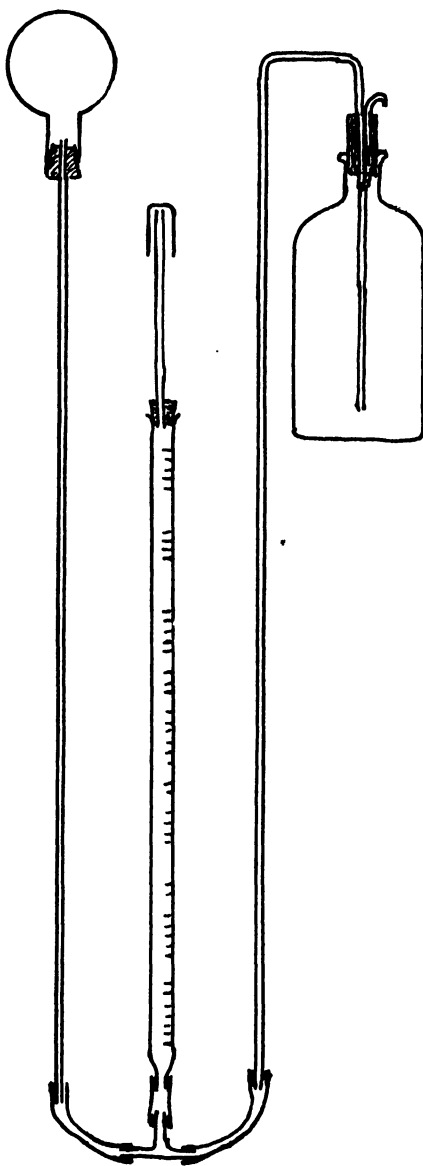
FIG. 4. Diagram showing arrangement of burette mounting for porcelain atmometers.

a horizontal file scratch (preferably blackened with ink or paint), which serves as zero mark when the reservoir is filled.

To install this simple mounting with bottle reservoir (fig. 3), a convenient procedure is as follows:—Remove mounting from reservoir and nearly fill latter with distilled water. Holding porcelain piece in left hand, with neck uppermost (never touch porous part with fingers), pour water from reservoir into it till it is filled to overflowing. Quickly set rubber stopper firmly into neck of porcelain piece, with pressure and rotation. Water rises in the supply tube. While meniscus is still in the tube pour more water from reservoir into tube till it overflows. Quickly invert mounting (now filled and bearing filled porcelain piece) and set it firmly into reservoir, which should be at least half full of water. With clean cotton and distilled water, sponge off the porous surface. Allow instrument to stand for 8–24 hours. Then lift mounting slightly and move it laterally till tube is in contact with bottle neck and lower surface of cork rests on bottle neck. Fill reservoir to zero mark with distilled water. Replace mounting and set cork firmly into place, being sure tube is vertical. Instrument is now in operation.—The aim of all this is to assemble bottle and mounting with no gas bubbles in tube or porcelain piece. If bubbles are seen in tube, or it is suspected that there are bubbles in the porcelain piece, remove stopper and repeat the whole procedure.

A burette graduated to 0.10 ml. serves as reservoir in another simple style, as shown in figure 4. This is especially suited to short-interval readings. The burette is closed above by means of a rubber stopper bearing a short glass tube, which is capped with a small vial. The top of this tube is below the level of the bottom of the evaporating surface and above that of the water in the extra water bottle when the latter is full. The cock below is temporarily opened to allow water to flow from bottle to burette when latter is to be refilled. If readings are to be interrupted for a time, the cock may be left open, so that the burette will not become emptied. The burette may be replaced by a finely graduated pipette, to give readings to 0.01 ml.; when such a pipette is used it may be attached to the bottle, which supports both it and the porcelain piece (Johnston and Livingston, '16). A potometer arrangement, by which an air bubble traverses a horizontal calibrated glass tube of small bore, as water is evaporated, is sometimes convenient instead of a burette (Wilson, '28).

To install a simple mounting with burette reservoir (fig. 4), the free end of the supply tube, bearing its rubber stopper, is temporarily lowered till tube slopes steeply downward from base of burette, and then stopper is firmly set into filled porcelain piece while distilled water is flowing through tube, cock being temporarily open meanwhile to prevent emptying burette.˙ Tube is then returned to erect position, with porcelain piece above.

An instantaneous-reading atmometer mounting was suggested by Johnston and Livingston ('16) and such instruments were subsequently constructed

and studied independently by Chalkley and Livingston ('29) and by Christiansen, Veihmeyer and Givan ('30). In its essentials, this peculiar mounting is the basis for the Chalkley-Livingston recorder already mentioned. With all other types, two consecutive readings (or an initial setting at zero and a subsequent reading) are required and the evaporational loss for the specified interval must be computed by subtraction; but with the instantaneous-reading instrument the current instantaneous rate of evaporation is read directly. Observation is made on a mercury manometer, which shows the current hydrostatic pressure in the enclosed space of the tube and porcelain piece. A resistance member of porous porcelain (a " soil-point cone ") is attached at the bottom of the supply tube, so that water entering the tube from the reservoir must pass through a fine-pored septum. For any given standardized septum any rate of water movement (i.e. of evaporation) corresponds to a certain hydrostatic pressure, or manometer reading, and the scale of the manometer is so calibrated as to give readings in terms of evaporation rates per hour. Although the evaporation rate usually fluctuates widely and rapidly, a glance at the scale shows the rate per hour that corresponds to the momentary current rate at the time of observation. Because of the magnitude of the temperature coefficient of the viscosity of water, however, the Chalkley-Livingston instrument is not reliable unless all observations are made with (or computed to) the same water temperature in the vicinity of the resistance septum. Water viscosity was neglected by Chalkley and Livingston and it remained for Christiansen, Veihmeyer and Givan ('30) to point out the practical as well as the theoretical necessity of this consideration. It is best to introduce a thermometer with its bulb close to the resistance cone, near the bottom of the reservoir bottle, and to correct all evaporation readings to the same temperature. The last-mentioned writers give useful tables of the viscosity of water in relation to temperature in this connection. To illustrate the importance of reservoir temperature, if an instantaneous-reading atmometer (with specified sphere and specified resistance member and with internal hydrostatic pressure—manometer reading—of 10 cm. of mercury column) loses water at the rate of 3.22 ml. per hour when the water temperature near the resistance member is 20° C., its evaporation rate would be 3.63 ml. per hour when the water temperature is 25° C. For a 5-degree temperature change the correction for viscosity difference is thus seen to amount to more than 10 per cent. Thus the manometer scale cannot be calibrated in terms of evaporation rate excepting for a specified temperature, nor would Chalkley and Livingston's suggested maximum-minimum instrument (after the fashion of a Six thermometer) be reliable unless the water temperature near the resistance were nearly constant at all times.

Non-absorbing mountings of many patterns (Harvey, '13, Livingston, '15, Livingston and Thone, '20, Thone, '24, Wilson, '30, Nichols, '23) have been designed to practically prevent downward movement of water through the supply tube during periods of precipitation, when there is free liquid water on the

outside of the porcelain piece.    One of the simplest and most common patterns has a Livingston-Thone ('20) valve attached to the lower end of the supply tube by means of a short coupling of heavy-walled rubber tubing; or the valve may be built into the tube.    The separable valve consists of a short glass tube about 5 cm. long, with bore of about 6 mm., containing about 0.5 gram of mercury held between two firm plugs of sheep's-wool yarn.    Downward passage of water past the mercury plug is practically prevented, but the slight suction of evaporation causes free upward flow around the mercury.

A porcelain piece equipped with non-absorbing valve sheds precipitation water as though the porous porcelain were water-proof.    When a bottle reservoir is used the cork must be tightly set into the bottle, not only to afford rigid support for the porcelain piece but also to prevent leakage of precipitation water into the reservoir around the cork.    The bent air-vent tube (fig. 3) allows air to enter but does not lead rain water into the bottle.

Bottle mountings with Livingston-Thone non-absorbing valves are set up as follows:—Attach valve to lower end of supply tube, using a heavy-walled rubber-tubing coupling about 2 cm. long.    Place valve under distilled water in nearly filled bottle and apply gentle suction at upper end of tube till latter is completely filled.    Then proceed as with simple mounting, being sure that rubber stopper is set firmly into porcelain piece while the latter is *below* the tube; if mounting is righted before stopper is forced into place the pressure applied in setting stopper is apt to expel the mercury and the lower plug.

To install Livingston-Thone non-absorbing valve in burette mounting (fig. 4), detach supply tube from bent rubber tube leading from burette and attach valve at lower end of supply tube as above.    Fill supply tube by suction, as for bottle mounting with valve, invert it and set stopper firmly into filled porcelain piece.    Then open cock and allow distilled water to flow from free end of bent rubber tube while the latter is slipped on to the free end of the valve, which is temporarily uppermost; avoid trapping air in tube.    Then right supply tube, so that porcelain piece is uppermost and valve is below, where it is interposed, in vertical position, in the water-supply line that leads from burette to porcelain piece.

## OPERATION OF PORCELAIN ATMOMETERS

A preliminary period of operation for several hours, or over night, is desirable after installation, to allow the water phase of the porous porcelain to reach equilibrium and also to show that the instrument is operating properly. It is also well to soak porcelain pieces for several hours in distilled water before installation and such soaking may make a preliminary period unnecessary.

Only distilled water is to be used in these instruments; solutes accumulate in and on the porcelain and tend to reduce or otherwise alter the porosity of the instrument.    This consideration is of great importance and it is cer-

tainly not worth while to attempt atmometric readings with atmometers employing porcelain, paper or cloth, unless distilled water alone is used. There may be a temptation to employ rain water or spring water, on the supposition that injury due to solutes may thus be delayed or may not occur. Even though considerable precision is not desired, distilled water should always be used, however. Of course solutes are not ever to be introduced into the distilled water used (as has been done sometimes to prevent freezing).

Porous-porcelain evaporating surfaces should be kept as clean as possible. Dust and other contamination may adhere to the wet surface and water-soluble substances may diffuse therefrom into the porcelain, also a soiled white sphere is more absorptive of radiation than is a clean one; as white pieces become discolored they resemble black pieces to a degree. Algae or fungi are apt to develop on the porcelain surface, altering the extent and the exposure of the surface and its capacity to absorb radiation. Such growths also tend to increase accumulation of dust, etc.

The evaporating surface should be sponged with distilled water at frequent intervals. A somewhat soiled piece may be dismounted and scrubbed with a stiff-bristle brush (such as a toothbrush or a hand brush), preferably while the piece is held under a tricking stream of distilled water. Sponging with alcohol (about 95 per cent., the impurity being just water) is sometimes more effective than sponging with water. (But alcohol is apt to injure the water-proof coating on the neck. The coating may be renewed by applying several coats of a cellulose lacquer.) If algae are troublesome an occasional sponging (while the porcelain piece is filled and in regular position for operation) with aqueous solution of mercuric-chloride (about 1 gram per liter) is sometimes useful. Atmometer cups prepared in this laboratory have all been treated by $HgCl_2$ solution and their walls contain a trace of that antiseptic.

Reading of these instruments consists in ascertaining just how much water has been evaporated during the preceding period of operation. Instruments equipped with bottle reservoirs may be weighed from time to time. It is sometimes desirable to prevent evaporation while they are being moved and weighed, which is conveniently accomplished by covering the porcelain piece with an inverted beaker or similar light-weight cover. The quick-reading instrument described by Johnston and Livingston ('16) is convenient for simultaneous weighing and volumetric reading.

A bottle reservoir is refilled to the zero mark, from a graduated cylinder or burette, and the volume of water required is the reading for the last interval. To refill bottle, loosen the cork, raise it slightly and move it laterally as far as tube will permit, so that lower surface of cork rests on upper surface of bottle neck, thus leaving opening for filling. When cork is returned to place after filling bottle to zero mark, the water meniscus rises somewhat above the mark, but should not reach the cork.

With burette or potometer reservoirs reading is simple, but the cock

must be temporarily opened from time to time to replenish the burette or to drive the potometer bubble back to a new zero setting.

The wool plugs of Livingston-Thone valves may require renewal occasionally, lest they become so fouled as to hinder their performance. To conserve time and avoid trouble, it is well to have a supply of extra valves and to replace the entire valve rather than just the plugs.

In selecting exposures for porous-porcelain atmometers, it is to be borne in mind that an atmometer really shows nothing but the integrated influence of all effective evaporativity components acting on it from the surroundings throughout an observation period, and that the form of instrument employed limits the manner of its exposure to the surroundings. As has been said, the Bellani plate presents its plane surface in just one direction, being properly exposed for wind effects only when horizontal, and for direct sunshine effects only when carried on a heliostat mechanism in such manner as to maintain the plane surface perpendicular to the direction of the impinging sunshine. It cannot be properly exposed to both wind and direct sunshine at the same time. Nevertheless, some students of the influence of sunshine on plants appear to think that environmental radiation may be satisfactorily taken into account if only its vertical component is considered. When that is really desired the horizontally placed Bellani plate is eminently suitable.

If cylindrical atmometers are obliquely placed, as already stated, they may have a proper exposure for effects of direct solar radiation but in that case they are not properly exposed for wind effects.

Spherical atmometers must be employed for uniform exposure to all environmental influences and in all directions. Consequently, porous-porcelain spheres are generally best, and other forms should be used only when specially required.

Micro-climatic differences between different points or locations are much more pronounced and much more common with respect to evaporativity than with respect to some other commonly measured ecological features, such as temperature, precipitation, air humidity. These atmometers are far more sensitive to small differences in low wind velocities than is any other climatological instrument—excepting perhaps the wet-bulb thermometer, with which it is difficult to secure a satisfactory integration for a period with fluctuating breeze. Vertical or nearly vertical air currents are markedly effective. While a single sphere may represent the general exposure of a small plant with rounded top and leaves exposed in all directions, a number of suitably distributed spheres are required if one wishes to study evaporativity in relation to a tall plant or a leafy tree. It needs simply to be remembered that an atmometer shows only the evaporational influences operating upon it from its immediate environment (see Pessin, '25).

With regard to plant transpiration, which is loss of water vapor from foliage, etc., it should be noted that the transpiration rate is controlled partly by internal conditions (such as degree of stomatal opening, capacity of tissues

to absorb impinging radiation, incipient drying) and partly by environmental evaporativity. The transpiration rate is seldom proportional to the rate of evaporation from an adjacently placed atmometer for any considerable period of time. This is partly due to alterations or fluctuations in the internal characteristics of the transpiring parts, but it is also related to the fact that the shapes of the transpiring surfaces are usually very different from that of any atmometer. In its transpiration rate the plant does not follow an adjacent atmometer's performance, just as it does not follow in growth rate the performance of an adjacent thermometer. As far as experimentation has gone, porcelain atmometers are more sensitive to wind fluctuation than most plants and black porcelain atmometers are more sensitive to sunshine fluctuation than many plants. These are among the important considerations that require attention in ecological instrumentation.

## STANDARDIZATION AND CORRECTION COEFFICIENTS

Correction coefficients are highly important. Because different porous-porcelain pieces of the same form may differ somewhat in internal characteristics (especially with respect to extent of evaporating surface), all pieces should be standardized. This is accomplished by operating them for two or more test periods along with several (preferably three) previously standardized and subsequently unused pieces of the same form, the latter being used as standards. Standards and pieces to be standardized are of course to be given the same treatment, which is accomplished by having all of them arranged in the same horizontal circle on a slowly rotating table (Livingston, '12, Nichols, '13). A convenient type of rotating table is built on a horizontally placed wheel assembly for a motorcycle side-car, the axle being set into a suitable tripod casting or wooden base. The platform may be of any convenient size; a table 2.5 m. in diameter cares for about thirty-six atmometers at the same time. A small light table (up to about 1 m. in diameter) may be built on an ordinary bicycle-wheel assembly. A rotating table may be driven by means of an electric motor with suitable belts and reducing gear, or—since motorcycle or bicycle bearings are almost frictionless—continuous rotation may be maintained by means of a simple horizontal air stream from an ordinary electric fan, so directed that the artificial wind acts on the bottles and porcelain pieces at a suitable angle. Spheres and cylinders should be upright and the flat tops of Bellani plates should be horizontal. All pieces should be at the *same height* above the table as well as at the *same distance from the center* of rotation. Speed of rotation is not important, but a single rotation should be completed in a few minutes at most, and the possibility of a troublesome amount of centrifugal acceleration is to be avoided. Standardization is best carried out indoors but it may be accomplished in the open in the absence of rain. It should be done with very weak light or in darkness, especially when black pieces are used. Readings are taken when

each piece has lost about 30–40 ml. or more. They should be accurate to about 0.1 ml. Simple bottle mountings (fig. 3) with grooved corks are generally used in standardization, and a reading is made by refilling the reservoir to its zero mark, from a burette. The reading of each standard piece is multiplied by the coefficient of that piece and the resulting corrected readings are averaged. Then this average is divided by the corresponding reading from each of the pieces to be standardized. The resulting quotients are the respective coefficients of those pieces, but additional accuracy is obtained by repeating the whole procedure. The coefficient marked on the base of any standardized porcelain piece prepared in this laboratory represents the mean of two consecutive standardizations, the results of which did not differ by more than 0.04. The two coefficients that are averaged generally differ by no more than 0.02. Correction coefficients are abstract numbers, calculated only to two places of decimals.

Every reading from a porous-porcelain atmometer in use is to be multiplied by the correction coefficient of the particular porcelain piece with which the reading was secured. By this means any reading is approximately homologized with all other readings secured with the same instrument or with other standardized instruments of the same type, at all times and places. It is to be remembered that readings from different types cannot be homologized and that each type of porcelain piece is standardized only for its own type. Most of the recently published atmometric records refer to standardized 5-cm. white spheres. Coefficients of cylinders usually lie between 0.65 and 0.71; those of spheres between 0.76 and 0.83; those of Bellani plates, between 0.97 and 1.04.

Black spheres prepared in this laboratory bear coefficients derived from standardization in darkness, against white standard spheres. They have also been standardized against black spheres on a rotating table in the open with summer sunshine, at Baltimore, and all have agreed, as to sunshine effects, within a maximal range of variability of plus or minus 0.03. When black and white spheres are operated side by side in the open and in darkness (by night) and each reading is multiplied by the corresponding coefficient, the corrected readings of the two should be alike within a plus or minus variability of no more than about 4 or 5 per cent.

Frequent restandardization of porous-porcelain pieces is desirable, because a correction coefficient may become significantly altered, as by soiling of the piece, in a period of operation. Nevertheless, carefully treated white spheres have in many instances maintained their original coefficients for many months of continuous operation in the open. Alterations of no more than 0.03 or 0.04 are generally to be neglected as insignificant, but when a rather high degree of precision is required restandardization should be as frequent as possible. In ecological instrumentation a good plan is to restandardize all instruments, or to introduce newly standardized ones, at monthly intervals or thereabouts. Restandardization procedure is the same as for the

standardization of new pieces. If one uses a large number of instruments it may be well to do one's own restandardizing, using as standards pieces whose coefficients have been directly or indirectly based on the standard of this laboratory. Maintenance of the standard is apt to be somewhat uncertain unless a relatively large number of pieces of the type in question are available. From 1,000 to 1,200 new white spheres have been standardized annually here in recent years and the supply of unused standardized pieces is usually large. No piece is used as standard for more than a few days, after which it is again standardized as if it were new. A table about 2.5 m. in diameter is now employed here, making about five rotations per minute. Many porcelain pieces have been temporarily returned to this laboratory for restandardization or reconditioning, or both, and a record is available of all standardizations carried out here in the last twenty-five years. Some pieces have been returned repeatedly.

Restandardization in the field is possible by occasionally operating, for a day or two at a time, a newly standardized piece (of the same type) beside the piece in question. The two instruments are of course to be given the same exposure, as nearly as possible. For example, suppose white sphere $A$, with original coefficient of 0.78, has been in operation for 30 days and that a new white sphere, $B$, with coefficient of 0.80, is operated beside $A$ for the 31st day. Suppose the readings for that day are 75 ml. ($A$) and 65 ml. ($B$). The second is corrected by multiplying by 0.80, giving 52 ml. as corrected reading for sphere $B$. Assuming that both instruments have had the same exposure and that 0.80 is the correct coefficient for sphere $B$, it is obvious that the coefficient of sphere $A$ has altered from 0.78 to 0.69 ($52/75 = 0.69$). This constitutes a considerable alteration and sphere $A$ should be retired, being replaced by $B$ or another newly standardized sphere. Had the test been made sufficiently earlier the alteration would have been less pronounced. On the supposition that the alteration of sphere $A$ has proceeded uniformly, its recorded readings for the preceding 30 days might be *recorrected,* as by using the original coefficient (0.78) for the first day only and using 0.77, 0.76, 0.75 . . . 0.69, as coefficients for succeeding 3-day periods. (The same sort of sliding-scale recorrection may be applied when the piece to be tested has been retired without field test and has been restandardized on the rotating table.) There is naturally no such thing as extreme accuracy in atmometric records, however, and recorrection must always depend on judgment. It is best to retire a porcelain piece before its coefficient has altered by more than about 0.03 or 0.04, replacing it with a newly standardized piece. Then recorrection need not be considered.. It must not be forgotten that the standardization of black pieces (spheres or Bellani plates) must be accomplished without considerable radiation; in the field this is done by means of night readings.

· In climatological studies it is well to operate instruments in triplicate, three side by side at each location, about 30 cm. apart and at the angles of

a horizontal equilateral triangle. The average of the three corrected values for each observation is used as the record of that observation. Then one sphere may be retired (for restandardization) every week or two, being replaced by a newly standardized one. The two unretired ones are thus tested by means of the new one, for the first day or two of its operation. For example, let spheres *A, B* and *C* operate side by side for two weeks, then replace sphere *A* with newly standardized sphere *D*. Two weeks later replace *B* with *E* and after two more weeks let *C* be replaced with *F*. Sphere *E* might be sphere *A* after the latter had been restandardized, etc. These examples will suggest many other useful ways by which relatively accurate data may be secured when coefficients alter to a considerable degree.

## RECONDITIONING PORCELAIN PIECES

If a porcelain piece appears to be seriously soiled or if its coefficient has altered (as shown by restandardization) by more than about 0.05, it is desirable that it be reconditioned and standardized again, as a new piece, before it is returned to operation. Prolonged soaking or heating in distilled water, with several changes of water, or percolation with distilled water, is useful as cleaning treatment in many instances. When the lacquer coating has been injured it is of course to be renewed by new applications; for this a good spar varnish is about as satisfactory as cellulose lacquer. Spots may sometimes be removed by rubbing with fine sand-paper or emery cloth.

The most satisfactory reconditioning treatment is to regrind the evaporating surface with sand-paper or carborundum or emery cloth. Spheres and cylinders are attached to a horizontal, electrically driven rotating spindle, or to the head piece of a lathe, by means of a suitable rod and rubber stopper. Bellani plates are best ground by rubbing them against a piece of carborundum cloth lying on the work bench, or by means of an electrically operated belt grinder. Serious alteration in the shape of the evaporating surface is to be avoided. After regrinding, a cylinder or sphere is of course somewhat smaller than before and consequently its coefficient may be somewhat larger. Each reconditioned piece is standardized as if it were new. " Restandardizing " (without any cleaning) gives coefficients for the correction of *past* records only. " Cleaning and standardizing " gives coefficients for *future* records only. " Restandardizing, cleaning and standardizing " gives corrected coefficients for *past* records and new coefficients for *future* records. Experience indicates that reconditioned pieces are generally as satisfactory as new ones; a sphere may be reground several times before its wall becomes too thin for satisfactory use. When pieces are sent from field to laboratory for restandardizing (for correcting *past* records) it is of course essential that they should *not* be cleaned at all before they are sent; they should be *thoroughly air-dried* and *well wrapped,* which is also true of pieces returned to the laboratory for reconditioning.

### Special Applications of Porcelain Atmometers

*Multiple Atmometers.*—It is sometimes desirable to arrange several like porcelain pieces so that all have sensibly the same exposure and all draw water simultaneously from the same reservoir. The actual amount of water lost from the reservoir in an observation interval would then be the sum of the unknown actual losses from the several pieces, and the average actual loss per piece would be obtained by dividing that sum by the number of pieces used. Such a multiple instrument is specially useful when losses from a single porcelain piece are apt to be too small to be measured with requisite precision. If the coefficients of all pieces are equal the average actual loss is naturally to be multiplied by the common coefficient. But when the individual coefficients are not alike it is of course mathematically incorrect to use their average as the coefficient of the multiple instrument, although the error arising from doing so is usually negligible when the several coefficients are nearly alike, as they should be. The true coefficient for a multiple instrument with *n* like spheres is *n* divided by the sum of the reciprocals of the individual coefficients. The average corrected loss per sphere is obtained by multiplying the total loss from all by one-*n*th of resulting quotient.

*Atmometry at freezing temperatures.*—This constitutes a special field of study (Livingston and Haasis, '29). Only the open-pan type of atmometer is at all suitable for obtaining useful records in times of freezing weather. With an open pan a non-freezing solution (of glycerin, NaCl, CaCl$_2$, or other non-volatile solute) may be used, but the same solution should be used throughout the whole period of study, for readings from a solution are not directly comparable with readings from water and comparisons by means of computation are not satisfactory. Pure water is added at frequent intervals, with stirring, to maintain a nearly constant level. Open pans of ice have been used sometimes, with proper precautions and technique, for studies confined to periods without thawing conditions. Because the vapor pressure of ice does not vary continuously with that of liquid water, readings from the liquid cannot be homologized with readings from the solid unless more or less uncertain computation is resorted to. Paper, cloth, porcelain or other water-impregnated solids are not at all suitable for atmometers to be operated in freezing weather.

Porous-porcelain atmometers are often broken or otherwise injured by short freezing periods, as on frosty nights. Although the rate of water loss during a freezing period cannot generally be measured as a useful atmometer reading, yet accidental frost breakage may be avoided by the use of a rubber tube sealed at the ends and coiled within the sphere, to supply an enclosed air chamber to "take-up" the expansion incident upon freezing of the water in the sphere cavity. These considerations have been discussed by Livingston and Haasis ('29).

*The radio-atmometer.*—This instrument gives an approximate measure

of the drying influence of radiation from sun, sky, etc., automatically integrated for each observation period. Direct sunshine constitutes the main component of this influence in many instances, but indirect sunlight (from clouds, etc.) sometimes exceeds direct sunlight. This instrument consists of two porcelain-sphere atmometers, one white and the other blackened or black, similarly mounted side by side and at the same level, about 20–30 cm. apart. They may be on a horizontal, continuously rotating table, so that one follows the other in a horizontal circular path, the two being 180° apart. For short-interval readings burette mountings, or mountings with pipettes or potometer tubes, are convenient. The *difference* between a corrected reading from the black sphere and the corresponding corrected reading from the white sphere is taken as a relative measure of the mean total effective intensity of radiation for the interval considered. The two corrected readings ought to be approximately alike for intervals of darkness or of very weak light. The radio-atmometer, as thus far developed, is not sensitive to differences in very weak radiation. For studies on the *vertical* component of radiation (when other components are neglected), a black and a white Bellani plate, horizontal and side by side (about 30 cm. apart) and at the same level, form a satisfactory radio-atmometer.

Multiple instruments are specially useful for radiation studies, several white spheres and the same number of black ones being exposed in the same horizontal circle, preferably alternating and on a rotating table. All white pieces draw water from one burette and all black pieces draw from a second burette.

*Atmometry in the study of room conditions.*—Because a suitable atmometer integrates all the drying influences of its surroundings for each observation interval, such an instrument offers an excellent means for studying air conditions in living rooms, laboratories, offices, greenhouses, etc. With standardized white porcelain spheres the evaporativity of rooms in this laboratory (about 1 m. above the floor, as on a table or bench) is usually about 0.8 ml. per hour in the winter, when artificial heat is present. Wilson ('28) has shown how different regions of the same greenhouse may exhibit marked differences in evaporativity.

### INSTALLATION AND OPERATION OF PAPER ATMOMETERS WITH HARD-RUBBER MOUNTING

Several forms of paper atmometers of the Piche and Cantoni types have been described (Livingston, '11). Enquiries from several investigators in different parts of the British Empire led to a series of attempts to devise an improved mounting for paper circles and paper cylinders, to avoid some of the difficulties encountered in the operation of available instruments of these types. The most satisfactory result of these attempts, in which the writer was efficiently aided by Dr. F. M. Hildebrandt and Dr. J. D. Wilson, is the

mounting shown diagrammatically in figure 5. It consists of a hard-rubber tube (*BB'*) 35 cm. long and 1.5 cm. in diameter outside, with 7-mm. bore, closed above by means of a hard-rubber cap (*A*) that bears a threaded pro-
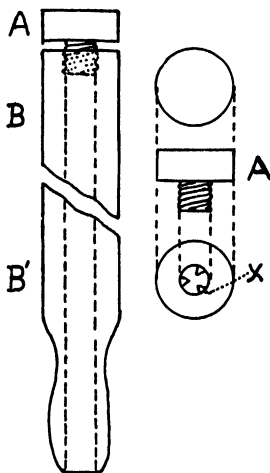


FIG. 5. Diagram showing arrangement of parts of hard-rubber mounting for paper-disk atmometers.

jection or plug below, by which it is screwed into the tube. The screw plug has three vertical lateral grooves (*X*) which connect the cavity of the tube below the plug with the space between the upper edge of the tube and the lower face of the cap. A disk of thick filter paper, with a circular central opening 7 mm. in diameter, is first placed on the lower side of the cap, the projecting threaded plug of the latter reaching through the opening. Then the cap is screwed loosely into the top of the tube. By means of a flexible rubber tube from a distilled-water reservoir at a higher level, water is led into the mounting at its lower end. The water level in the mounting rises, driving the air before it, till the entire mounting is filled and water flows out between tube and cap, saturating the paper. The cap is now screwed down into place, compressing the wet paper and holding it firmly. The reservoir is then lowered to bring its free water surface to a level lower than that of the paper. A burette reservoir arranged much as in figure 4 is very satisfactory for this instrument. As water evaporates from the paper it is replaced by upward movement through tube and cap grooves, and readings may be taken from time to time on the burette scale. The diameter of the paper disk is limited by the rate at which water can move outward laterally through the paper; if the edge of the disk tends to become dry in periods of rapid evaporation the disk used is of course too large. The paper disks now supplied are 5 cm. in diameter.

If difficulty is encountered in securing an air-tight seal where the wet

paper is seized between cap and tube, little washers or gaskets of paper like that of the disk, with outer diameter the same as that of the cap, are placed between disk and cap or between disk and tube, or both.

Instead of a paper disk one may use a cylindrical extraction thimble of thick filter paper, with flat bottom in which a 7-mm. opening has been cut at its center. The thimble is inverted and its flat bottom is seized between cap and tube, the cylinder extending downward around the latter. This arrangement provides a cylindrical paper evaporating surface, with an air space between the cylindrical paper wall and the outer surface of the hard-rubber tube within. This space may be nearly closed, and the paper cylinder may be steadied against wind pressure, by means of a suitable ring, as of waxed thread or fine copper wire, etc., wound upon the tube at the proper level. For many reasons paper atmometers are not generally satisfactory, but they are sometimes required in special studies.

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# POSTGLACIAL VEGETATION OF THE LAKE MICHIGAN REGION [1]

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Our knowledge of postglacial vegetation and of its migration in eastern North America is still scanty and uncertain. Much of this supposed knowledge has come from a study of existing forests with inference as to the past migration of tree species. Direct data are few and fragmentary. They have come mostly from such sources as fragments of wood and other plant material found in peat and in alluvial deposits. Some of the latter have yielded instructive results such as those obtained by Cooper and Foote ('32) from deposits in Minneapolis.

In Europe the knowledge of postglacial vegetation has advanced much farther than in America. Many criteria such as marine deposits, lacustrine beds and peat deposits have contributed to an explanation known for many years as the "Blytt-Sernander hypothesis" which postulates alternating periods of continental and oceanic climate with accompanying changes in the character of the vegetation of western Europe. Sears ('32) from his studies of the vegetation and the peat deposits of Ohio is inclined to believe that there were similar alternating dry and moist periods in the eastern North America.

Seeking for more exact information a group of Swedish workers led by von Post have examined peat deposits microscopically and finding in them well preserved tree pollen have elaborated a technique now well known under the designation "pollen analysis." Erdtman has been one of the foremost investigators in this field and has accumulated many valuable data ('22, *et al.*). He has made the technique internationally known and has devoted much attention to its improvement ('33, '34). Many European investigators have used this technique and there has accumulated a great mass of data indicated by the hundreds of titles listed by Erdtman ('27, '34) in his bibliography of the subject. The testimony of many investigators and some statistical observations have led to the acceptance of the data of pollen analysis as being reliable within certain limitations.

The results of many European investigators have seemed to strengthen the Blytt-Sernander hypothesis although the more recent tendency seems rather to favor and to strongly support von Post's ('30) three-fold division of postglacial time on a climatic basis into: (1) the period of increasing

[1] Presidential address before the Ecological Society of America at the Pittsburgh meeting December 28, 1934.

warmth; (2) the period of maximum warmth; and (3) the period of decreasing warmth.

It is not our purpose to discuss the technique of pollen analysis. Details of the process may be found in the contributions of Erdtman, Godwin ('34), Sears, Voss, and others. We may, however, examine some of the limitations to be observed in the interpretations of the results obtained by American investigators.

The pollens in the peat deposits may be classified with regard to their source on the basis of distance of transport as:

1. Pollen from trees growing on the bog and its immediate margin;
2. Pollen from trees in the forest within a radius of 1000 yards of the margin of the bog;
3. Pollen from trees between 1000 yards and 5 miles of the bog;
4. Pollen from trees more than 5 miles from the bog. These pollen components may be termed respectively the bog, regional, distant, and remote components. Von Post, Erdtman, and others have shown that the regional component is the largest and mo'st important of these, with the distant component second in size and importance.

This may explain how pollen analysis gives as a rule a general picture of the forest type for a rather wide area, not a representation of the local tree growth on the bog itself and its immediate margin. That is to say, the pollen diagram points to the general character of the forest-cover of the whole country side and this characteristic adds to its value as an indicator of the regional vegetation of past ages.

The pollen diagram must not be interpreted in detail, for the presence of a few scattered grains of any particular species cannot be accepted as proof that the species was growing in the immediate neighborhood of the deposit; they may have been windborne from a great distance. Hence they must be neglected unless the presence of the species in the vicinity is assured by other data. It should also be remembered that some tree genera produce much more pollen than others, that certain pollens are much better preserved in bogs and that certain tree genera, on account of their narrower ecological range, are much better indicators than others.

It is therefore evident that a pollen diagram (or diagrams) of an entirely unknown forest would not accurately reveal the composition of such a forest. But such diagrams would permit a choice to be made from a score of known forest types—the predominating type, or types, could be distinguished in spite of the fact that not all its tree components were represented in the pollen diagram, thus an abundance of *Abies* and *Picea* pollen in the Great Lakes region would make it most highly probable that *Larix*, *Betula*, and *Fraxinus* were also present in considerable numbers in the region adjacent to the bog, and that the forest was of the northern conifer type.

Since it has been impossible in past investigations to satisfactorily dis-

tinguish by their pollen the different species of *Pinus* and *Betula* occurring
in the Great Lakes regions, the record of these two genera has very limited
usefulness in interpreting the nature of postglacial forests. Both genera
extend from the northern to the southern limits of the area under consid-
eration and the different species differ widely in their ecological limits. It
should also be noted that pollen of *Populus*, *Taxus*, and *Larix* are seldom
well preserved and that *Acer* produces a relatively small quantity.

Non-tree pollens may be of decided importance in the interpretation of
the successional stages of a bog, but for the characterization of climate and
hence of vegetation as a whole, pollen of such large families as the Cypera-
ceae and Gramineae are of little significance since the different species occur
over such a wide range of habitats. Pollens of other herbaceous and shrubby
families have not proved to be useful since they are either poorly preserved,
negligible in quantity, or from plants of wide ecological limits.

## PRESENTATION OF RESULTS

Amounts of pollen are expressed in percentages of the total tree pollen.
It has been found impossible to express the amount of each pollen on an
absolute scale. It is therefore true that the amount of pollen from any one
species always affects the percentage values for all other species, hence
although the results do not show the absolute abundance of any one tree
but they do indicate changes in the relative abundance of the pollen of
different tree genera.

From the nature of the data it is most desirable that generalizations
based on pollen analysis should be made only upon very considerable accu-
mulations of evidence. In other words, the data from a single bog, even
though carefully collected, and accurately analyzed may be used for a gen-
eral picture of the surrounding forest only when supported by other data.
Such accumulations of data, until very recently, have been lacking in Amer-
ica and are still decidedly deficient. In the Great Lakes region of the
United States two groups of workers have contributed most of the pollen
analysis data from this locality, namely, Sears and his associates working
mostly in the vicinity of Lake Erie, and a group connected with the Univer-
sity of Chicago, investigating the peat deposits in the Lake Michigan region.
In the latter group Voss and Houdek are outstanding workers and to them
the writer is indebted for many data both published and unpublished. The
bogs of the Lake Michigan region are found mostly within the limits of
substages III and IV of the Wisconsin moraines (fig. 1). They cover a
north-south range of some 350 miles in the region of the transition belt
from deciduous to coniferous forest and comprise more than a score of bogs.
The portion of this region most intensively studied is that about the south-
ern end of Lake Michigan in substage III of the Wisconsin drift. There the
largest group of bogs is situated in the northeast corner of Illinois, within
the limits of Lake County, where Voss ('34) has given us pollen analyses of

seven bogs.   The present vegetation of several of these bogs has been de-
scribed by Waterman ('23, '26) and by Kurz ('28).   They are found scat-
tered in a rolling norainal area in a county that seems originally to have
had three-fourths of its surface covered with deciduous forests.



(AFTER LEVERETT, LEIGHTON, MARTIN.)
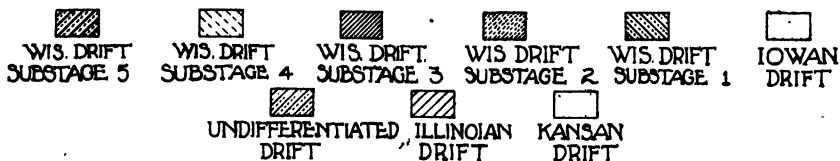
FIG. 1.   Map of the Wisconsin drift sheets.   Compiled by Voss.

The pollen analyses of these bogs show such remarkable agreement in their pollen diagrams that the results are most convincing. Two of these diagrams may be taken as representative of the group (figs. 2, 3). In inter-
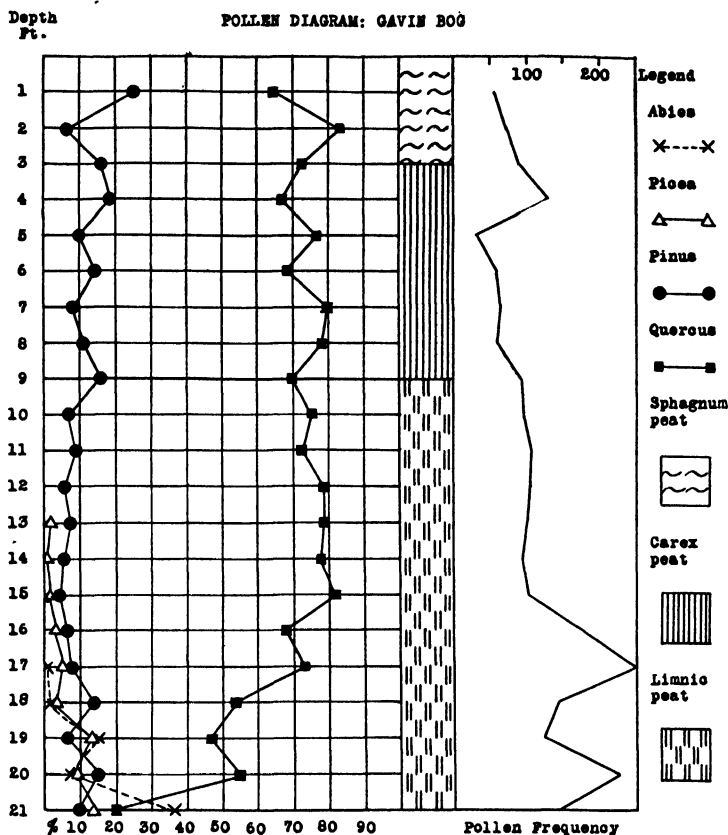


FIG. 2.    Pollen diagram of a bog in Lake County, Illinois.    After Voss.

preting these diagrams it must be remembered that the seven bogs, being in the same moraine and necessarily of similar age, differ considerably in depth. This necessitates some adjustments in the vertical length of the graphs in order to synchronize the records.

It may be instructive to make such adjustments and to compare the pollen curves for the same species in the group of bogs.

The balsam fir, *Abies balsamea*, may be regarded as a good indicator species. It is found represented by its pollen in all seven Illinois bogs at the bottom of the deposits. The pollen curves from the seven bogs plotted together (fig. 4) show an abundance of the species in the earliest centuries of the bog deposits but also show its disappearance relatively early in the history of the deposits. With our present limitations of knowledge it is

impossible to even approximate the time of the disappearance of *Abies* from the deposits and hence from the forests of Illinois, but if we accept the time of the recession of the last Wisconsin ice sheet as occurring some 25,000 years ago it seems likely that fir entirely disappeared during the first 4000
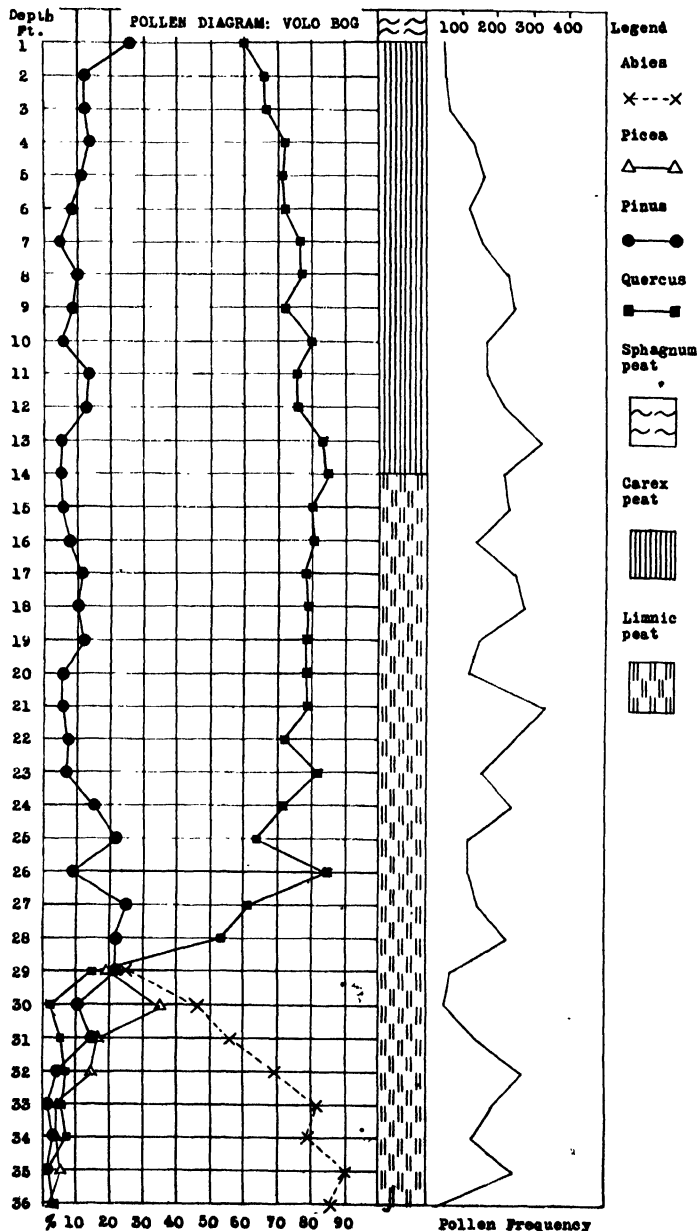


FIG. 3. Pollen diagram of a deep bog in Lake County, Illinois. After Voss.

or 5000 years or before the end of the first quarter of that period.    Data
from the bogs of northern Indiana, collected by Houdek ('33), although not
yet as abundant as that from Illinois, give exactly similar graphs for *Abies*.

These Illinois and Indiana bogs also show the early presence of spruce
in the forests of the region and apparently the genus *Picea* persisted for a
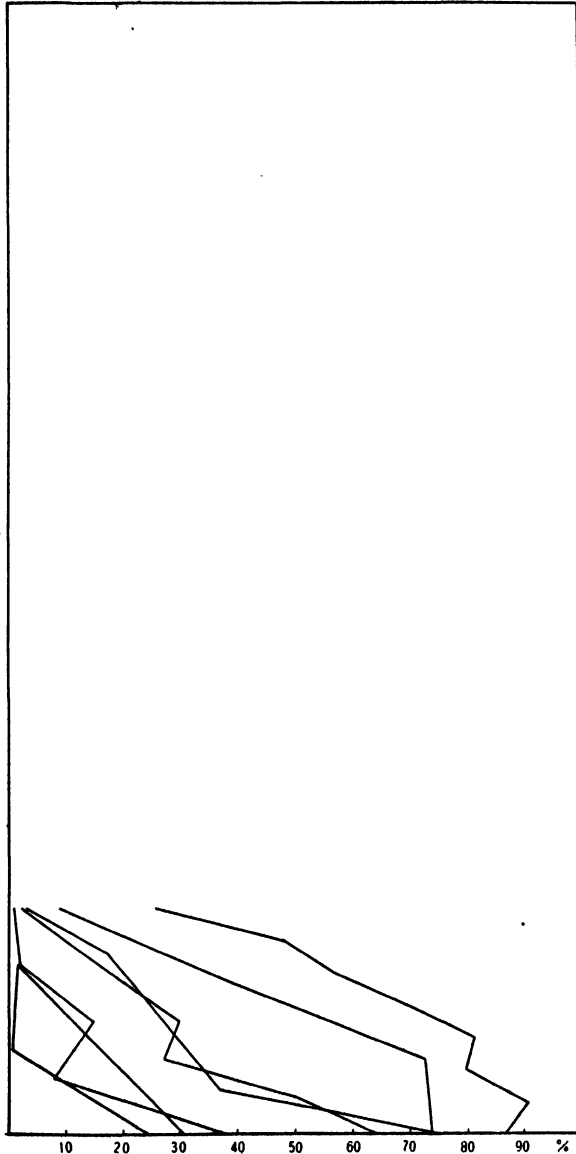


FIG. 4.    Graphs showing the occurrence of *Abies* pollen in seven bogs in Lake County,
Illinois.    Data from pollen diagrams by Voss two of which are shown in figures 2 and 3 of
this article.    Graphs represent depth vertically, percentage of pollen horizontally.

slightly longer period than did the fir but it also probably disappeared soon after the close of the first quarter of postglacial time. The curves representing the occurrence of *Picea* in the forests near all seven bogs are very similar (fig. 5).

In a bog in Wisconsin near the town of Waupaca in the same morainal
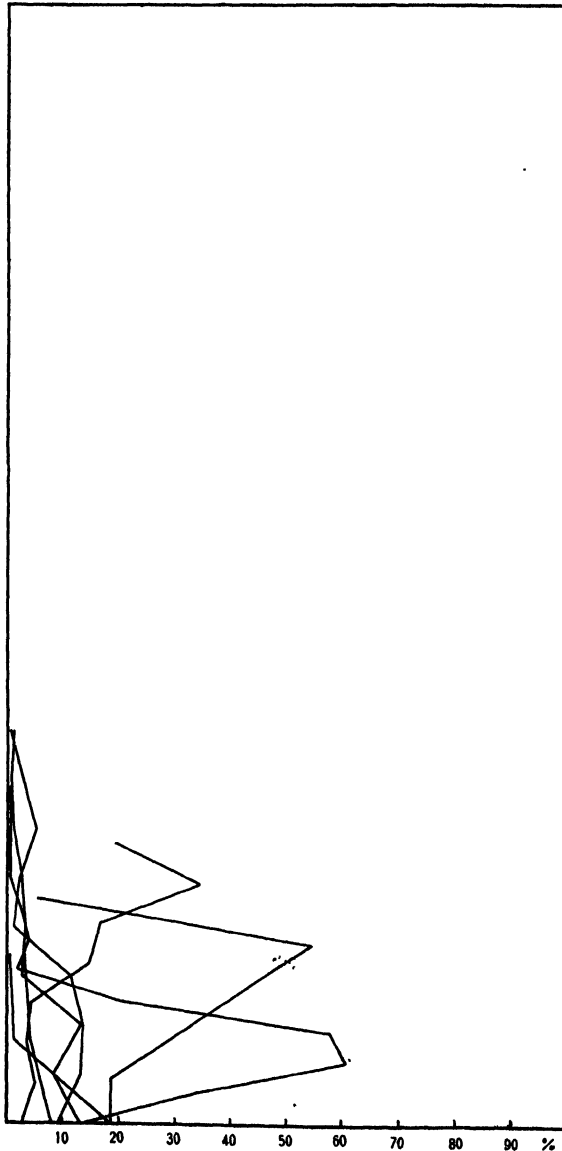


FIG. 5. Graphs showing the occurrence of *Picea* pollen in seven bogs in Lake County, Illinois. Data from pollen diagrams by Voss two of which are shown in figures 2 and 3 of this article. Graphs represent depth vertically, percentage of pollen horizontally.

deposits as the Illinois bogs, but 150 miles farther north near the mid-lake region, the *Abies* record is similar to that in Illinois but *Picea* persists throughout the entire postglacial period (fig. 6), while a bog in Minnesota 200 miles farther north near the shore of Lake Superior shows the persistence of both *Abies* and *Picea* throughout its record with *Picea* decidedly more abundant at the beginning and towards the close of the period than in the middle.
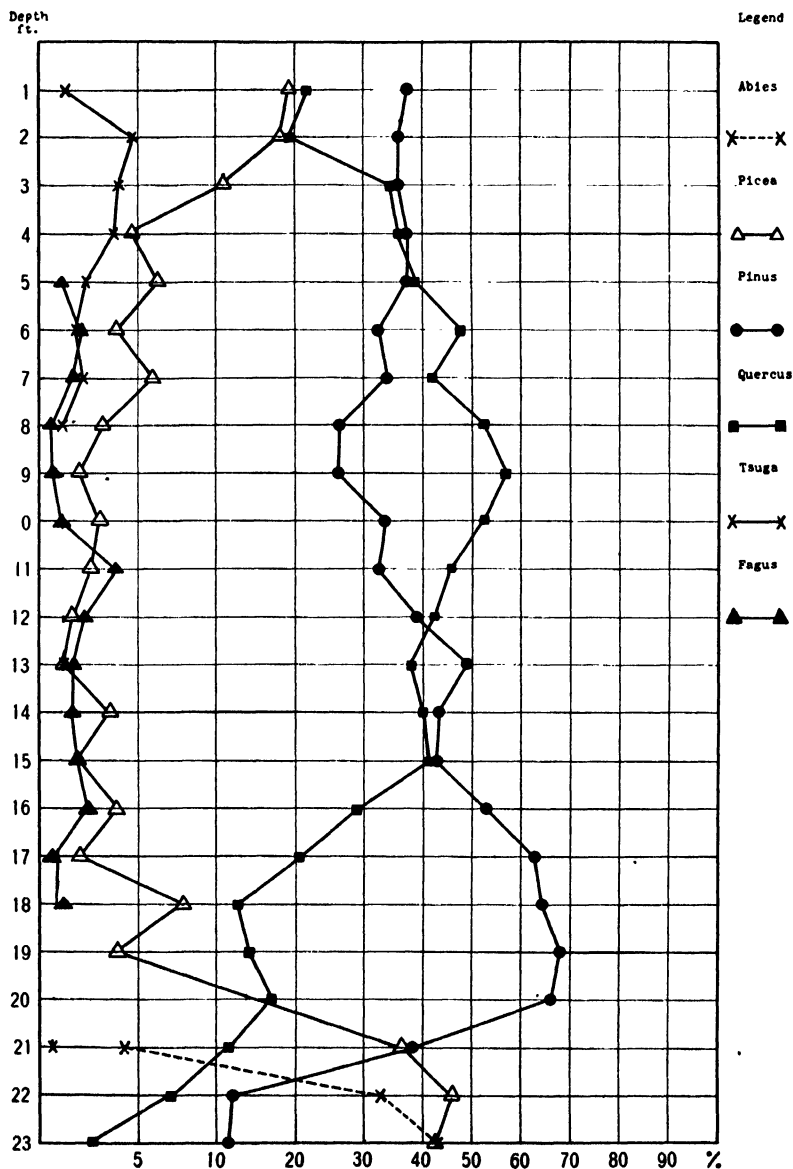


FIG. 6.   Pollen diagram of a bog in the mid-lake region of Wisconsin.   After data by Voss.

Similar pollen diagrams have been obtained by Houdek [2] and others from bogs in the lower peninsula of Michigan near the mid-lake region.

Two records from the Douglas Lake region 250 miles north of the southern end of Lake Michigan in the lower peninsula show *Abies* and *Picea*
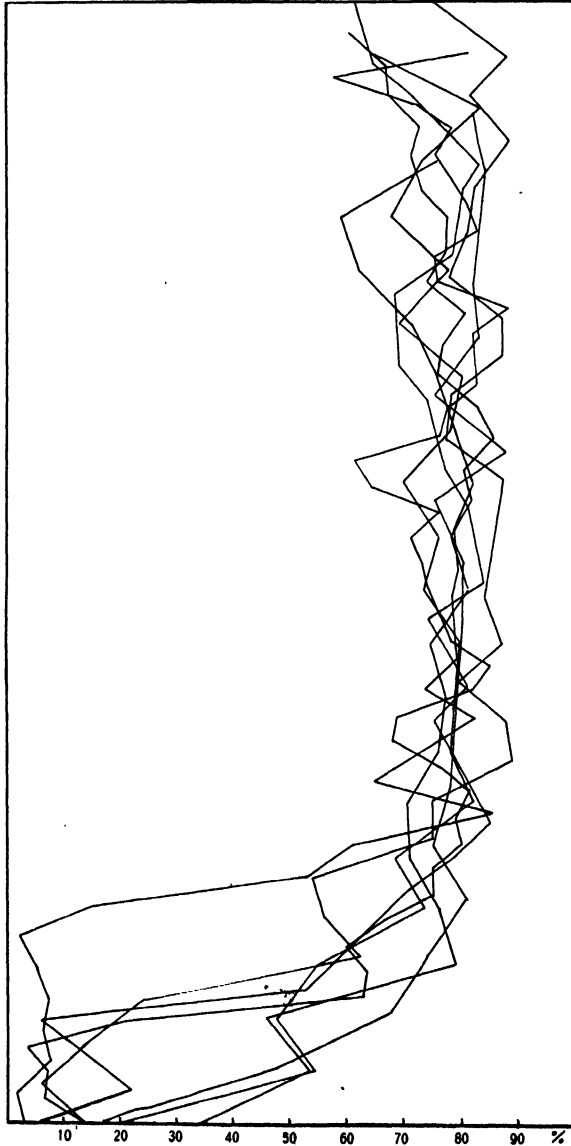


FIG. 7. Graphs showing the occurrence of *Quercus* pollen in seven bogs in Lake County, Illinois. Data from pollen diagrams by Voss two of which are shown in figures 2 and 3 of this article. Graphs represent depth vertically, percentage of pollen horizontally.

[2] Unpublished data.

persisting throughout postglacial time but least abundant during the middle half of the record.    *Quercus* is found in small amounts at the beginning of the record, in considerable abundance about the middle of the period diminishing towards present time.    Only in these diagrams does *Pinus* seem of significance, being most abundant towards the beginning and towards the end of the period.
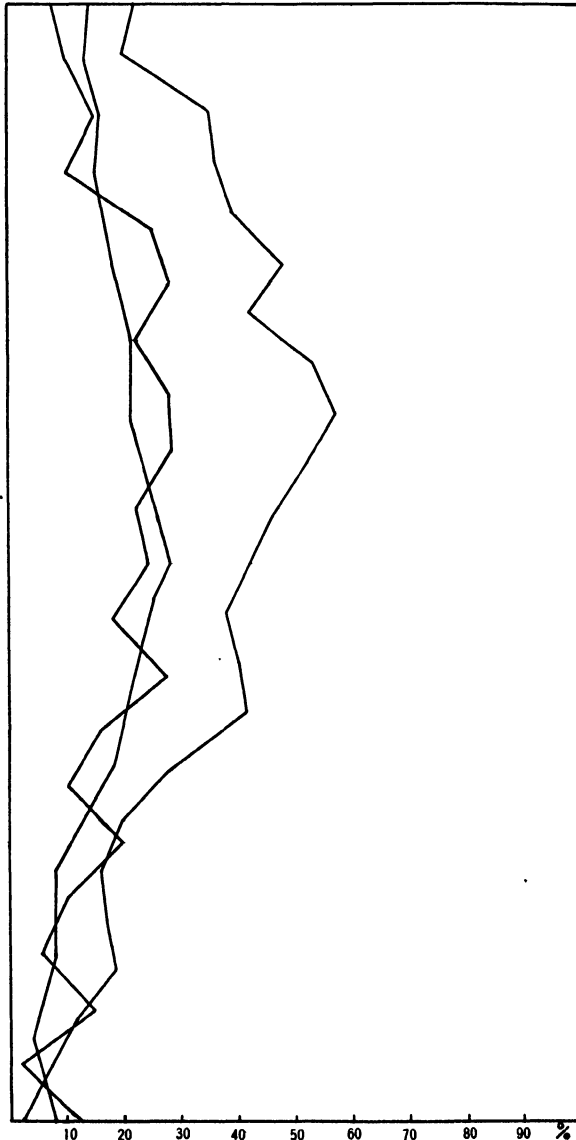


FIG. 8.   Graphs showing the occurrence of *Quercus* pollen in a Wisconsin and two Michigan bogs, all in the mid-lake region.   After data by Voss and Houdek.   Graphs represent depth vertically, percentage of pollen horizontally.

As an indicator genus *Quercus* seems to rank with *Abies* and *Picea* as very significant. Its pollen appears in all the bogs of the Lake Michigan region that have been investigated. The pattern of its graphs is strikingly different from those of the fir and spruce but this pattern remains very constant throughout all the Illinois and Indiana bogs (fig. 7). It is found in small quantities at the bottom of the deposits, reaches a maximum about the time that the fir and spruce disappear and persists with irregular fluctuations to the present. Quite a different graph pattern comes from the *Quercus* pollen record from the bogs of the mid-lake region of Lake Michigan. Here a decided maximum of oak is seen to be indicated during the middle half of postglacial time (fig. 8).

No other tree genera give records comparable in importance to those of *Abies*, *Picea* and *Quercus*. The *Pinus* record would indicate the presence of the genus throughout practically the entire postglacial period with no decided or regular times of maxima or minima. *Carya*, in the Illinois bogs roughly parallels *Quercus* with much smaller percentages of pollen. *Tilia* and *Acer* show a wide distribution both in time and space, but present narrow and irregular pollen curves that are difficult to interpret. The Wisconsin bog cited has a significant and well marked deposit of beech pollen extending from the 5th to the 18th foot of a bog which was 23 feet deep. This record may be regarded as extending through the middle portion of postglacial time and it seems to afford the most definite evidence, coming from the pollen records, of a decidedly warmer climate during the middle of the postglacial period. It may also be taken to indicate decidedly continuous mesophytism, equal to that obtaining at present. It is also interesting to note the occurrence of *Tsuga* pollen in the record of the upper half of the same Wisconsin bog.

## INTERPRETATION OF THE RECORDS

In attempting to translate the bog records into terms of climate and actual vegetation we are faced at the very beginning with the question of whether the forests followed closely upon the margin of the retreating ice sheet or whether a rather extended period of tundra vegetation intervened. Certain facts, however, seem to indicate that there was no wide interval between the ice and the forest. Voss ('33) has shown that throughout most, if not all of the last interglacial period, the Sangamon, which immediately preceded the late Wisconsin ice, much of central and northern Illinois was occupied by a coniferous forest similar to that which is now found north of Lake Superior. Further he has found that some bogs of northern Illinois, in moraines some 8000 years older than those in Lake County, have pollen diagrams similar to those of Lake County.[3] This would seem to indicate that there were forests within 50 miles of the edge of the ice sheet that laid down the terminal moraine in which the Lake

[3] Unpublished data.

County bogs are located. It therefore seems possible and perhaps probable that these forests retreated before the advancing ice sheet and in turn closely followed its recession. At least there is nothing in the bog records opposed to this supposition and the oldest deposits in the bogs of the Wisconsin moraines in Lake County, Illinois, and also the oldest deposits in much older bogs in adjacent parts of northern Illinois indicate the presence, in the vicinity, of just such northern forests as those which prevailed in the Sangamon interglacial period.

This forest seems soon to have been invaded by a deciduous element and probably before a fourth of postglacial time had elapsed the forests around the southern tip of Lake Michigan had assumed an aspect and composition very similar to those existing at the coming of the ax of the white man. The record seems to show that for some three-fourths of the postglacial period (perhaps for 15,000 years) oak-hickory forests with an admixture of elm, basswood, and a small amount of maple have occupied the morainic uplands of northern Illinois and southern Wisconsin. Pines were also present in small amounts perhaps on the poorer and sandier soils as at present.

In Indiana the forests seem to have been in the past as in the present somewhat more mesophytic as indicated by the appearance of the beech almost as soon as the fir and spruce disappeared.

As in Illinois, the chief characteristic of the record for the latter three-fourths of the period is its general uniformity. No variation in the pollen diagram is great enough to indicate a decided climatic or vegetational change. In fact, the only indications of climatic change in the pollen records of the northern Illinois and Indiana bogs is a maximum of *Fagus* pollen towards the middle of Indiana records and a slight decrease in *Quercus* pollen in one or two Illinois bogs, during recent centuries.

As fewer of the Wisconsin, Michigan, and Minnesota records have been uncovered, there is more uncertainty regarding their earlier forests. Coniferous forests of fir, spruce, and pine seem to have come first in all localities. The oak appeared early in Wisconsin and Michigan and is irregularly present in small quantity in the Minnesota records. In the Wisconsin record the oak reaches a decided maximum during the middle of the period which is also characterized by the presence of *Fagus*. *Tsuga* appears in the Wisconsin bog only during the last half of the period (fig. 6), which would seem to indicate that it was not originally a member of the coniferous forest. The Wisconsin record would therefore indicate that the middle of the postglacial period for scores of centuries showed no appreciable change of vegetation or of climate while increase of spruce and pine pollen with a corresponding slight decrease in the amount of oak pollen seems to indicate that a gradual cooling of climate occurred during the last centuries of the period that resulted in a decrease of the deciduous element in this transition area.

The maximum of *Fagus* pollen throughout the middle half of the Indiana records and its presence in the Wisconsin record during the same time inter-

val (fig. 6) would tend to indicate that the mid-postglacial climate was at least as mesophytic as that now existing.

The pollen records now available would indicate that the vegetation of the lower peninsula of Michigan has changed very little during the last half of postglacial time. It seems very probable that the climax forest has remained essentially similar to those described by Quick ('24) for his Regions IV and VI, and has been one dominated by maple, beech, yellow birch, and hemlock.

Certain studies of existing forests, notably those of Lee ('24) in Minnesota, also seem to indicate that the spruce-fir climax is slowly invading the deciduous    It therefore seems safe to venture the opinion that the transition belt of the conifer-deciduous forest was perhaps some 100 miles farther north towards the middle of postglacial time than at the present.

## CONCLUSIONS

The pollen record in the Lake Michigan region seems to show no evidence of alternating moist and dry periods during postglacial time.

A threefold division of postglacial time on a climatic basis as postulated by von Post seems fairly well marked in the mid-lake records, viz. (1) a well marked period of increasing warmth; (2) a long period of maximum warmth; and (3) a poorly emphasized period of decreasing warmth.

There seems to have been a corresponding threefold division of forest development during postglacial time, viz. (1) a period of the establishment and relatively rapid decrease of the northern conifer type; (2) a long period characterized by little change and the relative dominance of deciduous forests; and (3) a rather poorly marked period of slight increase of the northern coniferous element and a corresponding decrease of deciduous species.

The ice sheet seems to have been rather closely followed by a forest similar to the existing northern conifer forest in which spruce, fir, and pine were notable genera.

This forest seems to have been replaced in Illinois and southern Wisconsin, before the end of the first quarter of postglacial time, by a mixed deciduous forest in which oak, hickory, maple, and elm were dominant trees. This deciduous forest seems to have continued, relatively unchanged throughout the later three-fourths of postglacial time.

The mid-lake region of Wisconsin seems to have had throughout a mixture of coniferous and deciduous (oak-hickory-maple) forests similar to those now existing in the northern part of the state. A somewhat milder climate during the middle half of the period is indicated by the presence of more beech than now exists. Spruce seems to have increased slightly during the last score of centuries.

Throughout the latter three-fourths of postglacial time the forests of northern Michigan seem to have been very similar to those of the present; a climax of maple, beech, hemlock with pine on the poorer soil. A small

increase of conifers is indicated during recent centuries and also the invasion of a southern element in the southern part of the state.

The records for Wisconsin, Minnesota, and northern Michigan are as yet too fragmentary to permit them to be used as a basis of anything other than very tentative conclusions regarding the vegetational history of those areas.

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# TYPES OF NORTH AMERICAN POLLEN PROFILES [1]

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The following paper presents in graphical form a comparison of some twenty pollen spectra of peat bogs lying between the 65th and 107th meridians, and the 34th and 50th parallels. A set of seven transects has been prepared, three running from north to south, the remainder from east to west, as indicated in the map (fig. 1). Each transect has been assigned a Roman numeral and each station an Arabic number for convenience of reference.

The following stations are used in the present study:

1. Peat bog near Matamek River, 15 miles northeast of the mouth of the Moisie River on the north shore of Quebec. Position about 50° N., 66° E., 500 miles northeast of Montreal. Estimated age, under 2500 years. Described by Bowman ('31). Percentages have been recalculated to omit spores of cryptogams.

2. Mulgrave Bog (Auer, '30), near the Strait of Canso which separates the main part of Nova Scotia from Cape Breton Island. Position between 45–46° N., 61–62° W. In this, as all of Auer's data, analyses were made at half-metre intervals.

3. Caribou Bog (Auer, '30), near the Bay of Fundy on the northwest shore of Nova Scotia. Position about 45° N., 65° W.

4. Spruce Swamp, between Kingston and Fremont, New Hampshire. Position about 43° N., near 71° 5' W. Material collected by L. Washburn, analysis made by M. Kaeiser. Unpublished data on file at the University of Oklahoma.

5. Dismal Swamp (Cocke *et al.*, '34), on Jericho Ditch between Lake Drummond and Suffolk, Virginia. Position about 36° 40' N., 76° 30' W.

6. Peat bog between Holston and Iron Mountains, at an elevation of 2800 feet, in Johnson County, at the eastern end of Tennessee. Former beaver dam and lake. Position about 36–37° N. 82° W. Material collected by A. J. Sharp, analysis by C. Still. Unpublished data on file at University of Oklahoma.

7. Bear Meadows, Center County, Pennsylvania, not far from State College. Position south of 41° N., east of 78° W. Collection and analysis by P. B. Sears, data unpublished. Apparently a beaver-made lake.

8. Welland Bog (Auer, '30), near Welland, Ontario. Position about 43° N., 79° W.

9. Clair Bog (Auer, '30), near Levis, opposite Quebec, Canada.    Position about 47° N. 71° W.

10. Peat bog on Ferguson Highway to Timagami, about 34 miles north and slightly west of North Bay, Ontario.    Position about 46–47° N.,
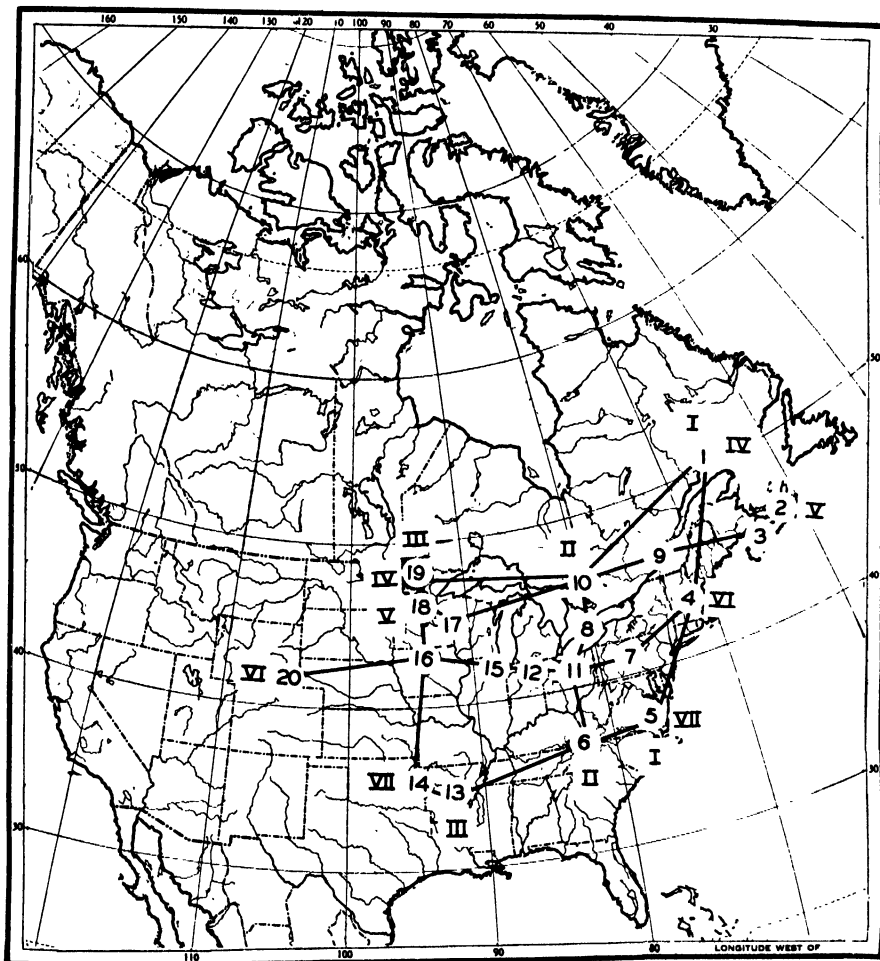


FIG. 1.    Map of North America, showing the approximate location of the stations, 1–20, and the system of transects, I–VII, which serve as a means of comparing pollen profiles at the various stations.

79–80° W.    Collection and analysis by E. Janson and E. Halfert, to whom acknowledgment is due for gracious permission to use data in advance of publication.

11. Mud Lake (Sears, '31), in eastern Ashland County, Ohio, combined with the profile of the older Bucyrus Bog (idem '30) in Crawford County. General position, 40–41° N., 82–83° W.

12. Center Lake (Houdek, '32), one mile northwest of Angola, Stueben County, Indiana. Position about 41–42° N., 85° W. This is a glacial depression lying outside the beach lines of Lake Chicago.

13. Dark Hollow (Sears and Couch, '32) cypress swamp, now drained, near North Little Rock, Arkansas. Position 34–35° N., 92–93° W. Probably not very old. Top two feet destroyed by fire.

14. Pond excavated by moundbuilders in Arkansas River Valley near Spiro, Oklahoma, just west of Fort Smith, Arkansas. Position 35–36° N., 94–95° W. Silt collected by Forrest Clements and Sears, analyzed by M. Bjerregaard. Unpublished data on file at University of Oklahoma. This short profile probably represents a period of less than 1000 years.

15. Volo Bog (Voss, '34), in Lake County, Illinois. Position about 42–43° N., 88° W.
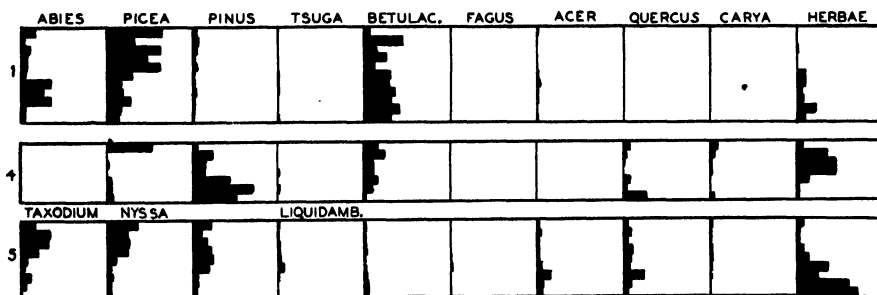


FIG. 2. Comparison of pollen profiles at three stations along the Atlantic coast: 1, Quebec; 4, New Hampshire; and 5, Virginia. Note complementary character of grass-sedge swamp and forest. Transect I.

16. East McCulloch peat bed (Lane, '31), in Twin Lake Township, Hancock County, Iowa. Position about 43° N., 93–94° W.

17. Hayward Bog (Voss, '34), near Hayward, Sawyer County, in northwest Wisconsin. Position about 46° N., 91–92° W.

18. Bay Lake Bog (Voss, '34), in Section 27, Bay Lake Township, Crow Wing County, Minnesota. Position about 46–47° N., 94° W.

19. Coleraine Bog (Voss, '34), near Coleraine, Itasca County, Minnesota, along the Great Northern Railroad. Position 47–48° N., 94° W.

20. Peat deposit near Snowy·Range, Medicine Bow Mountains, in southeast Wyoming, about 45 miles west of Laramie. Position 41–42° N., 106–107° W. Collection and analysis by Sears. Data unpublished.

Utilizing these 20 stations transects have been constructed as follows:

I. Stations 1, Matamek, Quebec; 4, Spruce Swamp, New Hampshire; 5, Dismal Swamp, Virginia, being thus a line extending southwestward very close to the Atlantic coast. In fact each of the deposits has been affected by changes in waterlevel due to coastal movements. This is reflected in the considerable representation of herbaceous pollen at levels marked

by maximum swamp conditions. The edaphic record incident to develop-
ment from grass swamp to forest is the outstanding fact in each profile.

II. Stations 10, North Bay, Ontario; 8, Welland, Ontario; 11, Mud Lake
and Bucyrus, Ohio; 6, Johnson County, Tennessee, being thus on a line in
the vicinity of the 80th meridian. The combined Ohio profile here repre-
sents a much longer period of time than any of the rest—perhaps as much as
10,000 years.
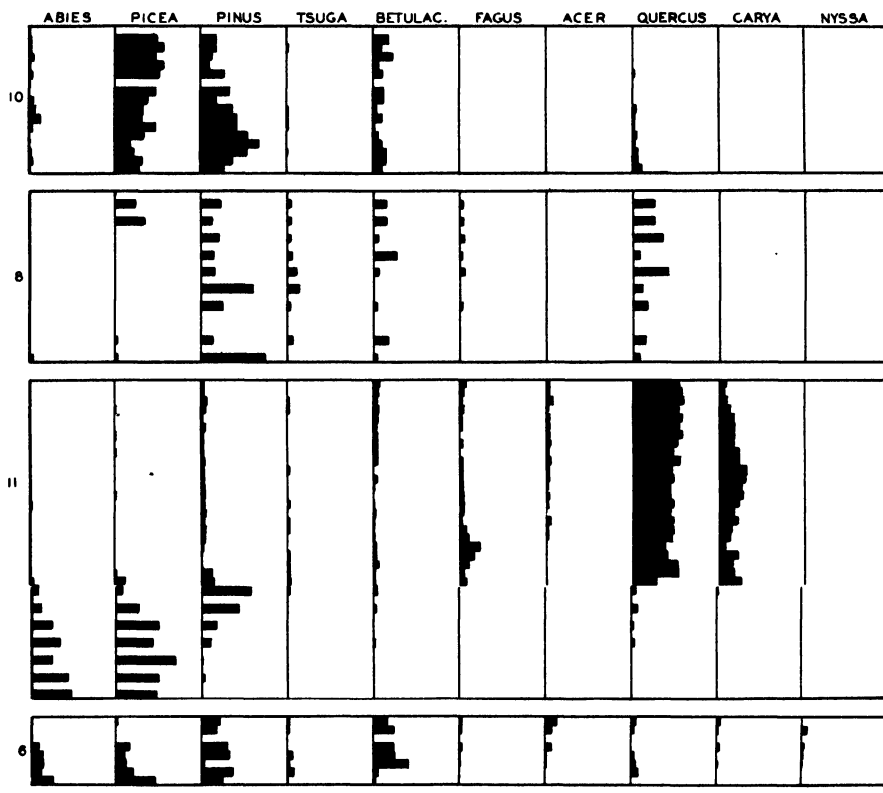


Fig. 3. Comparison of pollen profiles at four stations in the vicinity of the 80th
meridian: 10, East central Ontario; 8, Southern Ontario; 11, North central Ohio; and 6,
Mountains of eastern Tennessee. The largest segment of postglacial time is shown in 11,
a combined profile. Note maximum of oak in 10 and 8, and of hickory in 11; also recent
increase of spruce and pine in the two former. Note change in composition from north to
south, and effect of altitude in 6. Transect II.

III. Stations 19, Coleraine, Minnesota; 18, Bay Lake, Minnesota; 16,
Hancock County, Iowa; 14, Spiro, Oklahoma; and 13, Little Rock, Arkansas,
being thus a line in the vicinity of the 94th meridian. The two last deposits
are relatively recent and shallow, while the Iowa material is much more
compact in proportion to its age than that from Minnesota, both because of
recent drainage, and the drier prairie climate in which it developed.

IV. Stations 1, Matamek, Quebec; 10, North Bay, Ontario; and 19, Coleraine, Minnesota, being a line east and west in the vicinity of the 47th to 50th parallels.

V. Stations 2, Mulgrave, Nova Scotia; 3, Caribou, Nova Scotia; 9, Clair, Quebec; 17, Hayward, Wisconsin; and 18, Bay Lake, Minnesota, being a line east and west in the vicinity of the 46th parallel.
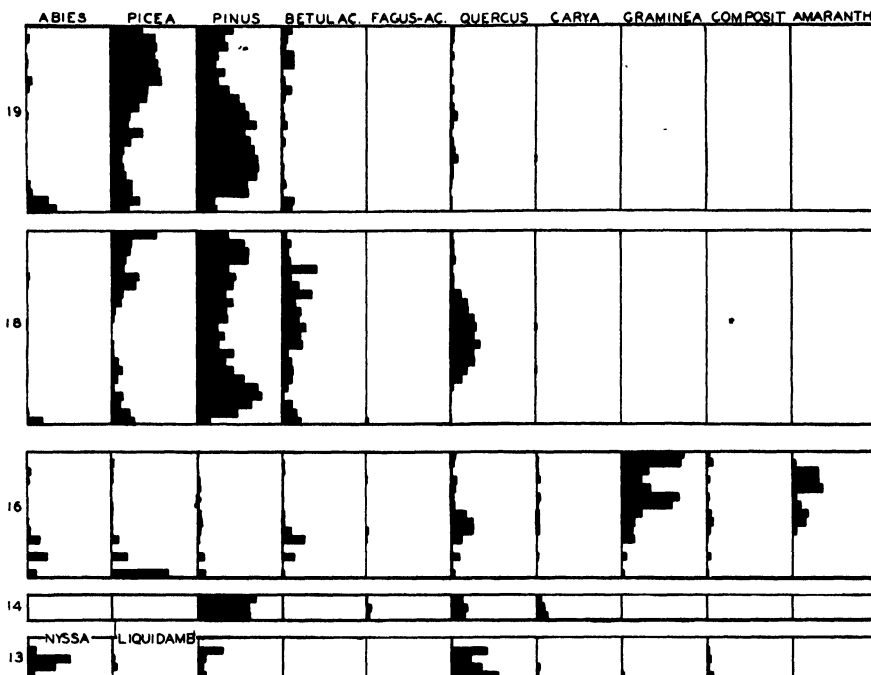


FIG. 4. Comparison of pollen profiles at five stations in the vicinity of the 94th meridian: 19, Northern Minnesota; 18, Central Minnesota; 16, Northern Iowa; 14, Eastern Oklahoma; and 13, Central Arkansas. Note general continental character of this chart. Oak maximum in 19 and 18 probably correlates with amaranth maximum in 16. Stations 14 and 13 are chiefly of interest because of composition. Transect III.

VI. Stations 4, Spruce Swamp, New Hampshire; 7, Bear Meadows, Pennsylvania; 11, Mud Lake and Bucyrus, Ohio; 12, Center Lake, Indiana; 15, Volo, Illinois; 16, Hancock County, Iowa; and 20, Snowy Range, Wyoming, being an east and west line ranging between the 40th and 43rd parallels.

VII. Stations 5, Dismal Swamp, Virginia; 6, Johnson County, Tennessee; 13, Little Rock, Arkansas; and 14, Spiro, Oklahoma, being an east and west line in the vicinity of the 35th parallel.

In the diagrams spectra for the various stations on each transect are arranged vertically, in order to permit ready comparison. The various columns are appropriately labelled. Within a given profile each column represents depth vertically, percentage horizontally. Each bar in the graph

represents a depth of approximately one foot, except in those graphs based on Auer's data which omit alternate bars, and there the intervals represent ten inches.     The length of each bar is in proportion to the percentage of the particular pollen represented, the total width of each column being reckoned as 100 per cent.

Not every graph represents a complete pollen analysis of its station. Kinds of pollen not considered important for comparative treatment have in some cases been omitted.     Furthermore, the diversity of sources consulted makes absolute uniformity quite out of the question.     Some authors disregard all but tree pollen, others have published no tables, only graphs. Not all have employed the same criteria in calculating percentages, but this has been taken care of to some extent.     Nor is there any way to overcome the subjective differences due to variations in technique or to uncertainties of identification.
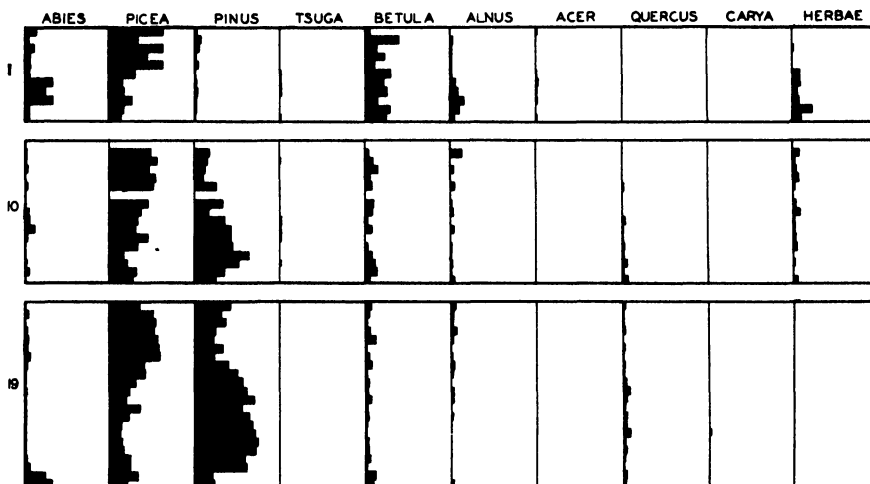


Fig. 5.   Comparison of pollen profiles at three stations ranging east and west between the 47th and 50th parallels; 1, Quebec; 10, Ontario; and 19, Minnesota.   Note shift from fir-spruce oceanic type 1 to spruce-pine continental type 19 and record of change from grass-sedge-alder swamp in 1, to noticeable oak maximum in 10 and 19.   Recent increase in spruce in all.   Transect IV.

Obviously some of the profiles represent a much longer segment of postglacial time than others.     Equivalent depths do not always measure equivalent time intervals, although there is undoubtedly a rough correspondence under similar climatic conditions.     For the Erie Basin a conventional figure of 25–30 years per inch has been obtained (Sears and Janson, '33).     In the subalpine bogs of southern Wyoming one inch appears to represent 10 years or thereabouts (Sears, '34).     In cases where bogs have been compacted by drainage or damaged by fire or weathering, either on top, or at some level below, thickness is naturally no criterion of age.

The axiom of the jurist, "*De minimis non curat lex*," is a dangerous one for the scientist to adopt, despite the beautiful use to which its principle is put in the calculus. In the present case there is no recourse but to apply it. Disregarding the inconsistencies and deficiencies just mentioned, inspection
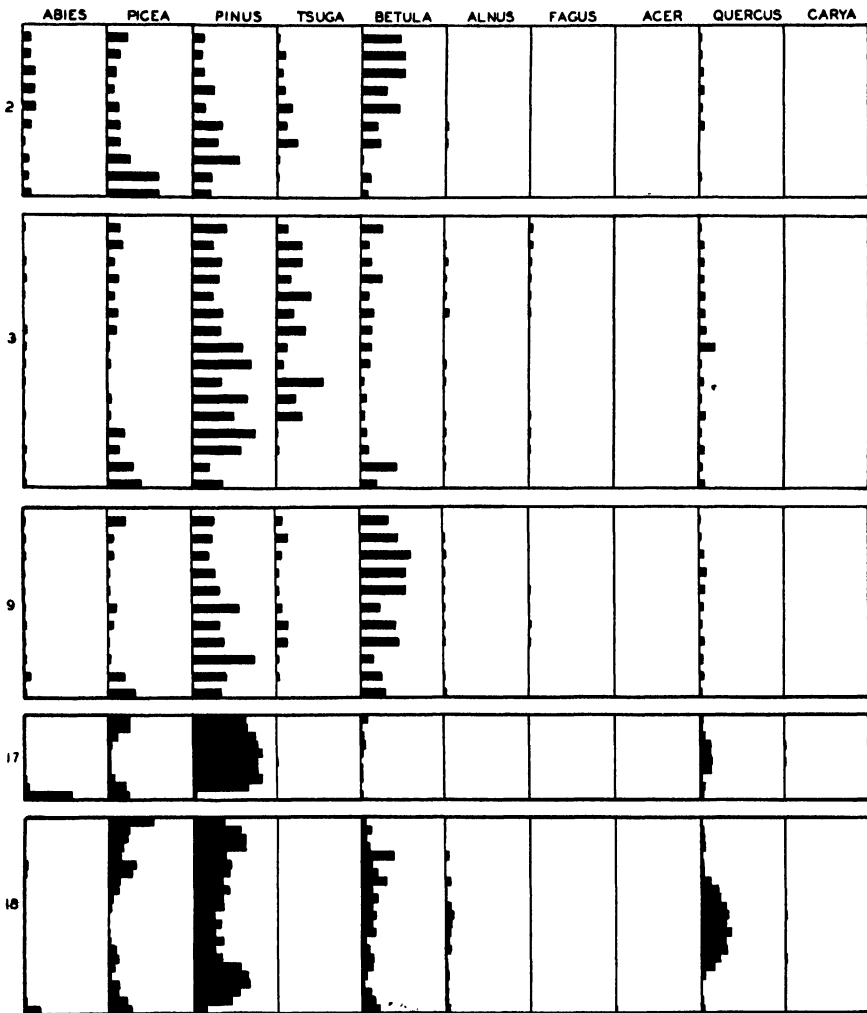


FIG. 6. Comparison of pollen profiles at five stations near the 46th parallel: 2, Eastern Nova Scotia; 3, Western Nova Scotia; 9, Quebec; 17, Northern Wisconsin; and 18, Minnesota. Top to bottom shows shift from oceanic to continental conditions. Oak maximum followed by return of spruce clearly marked in every case. Transect V.

of the graphs reveals certain broad tendencies which can be compared and interpreted, and which may give direction to the laborious and intensive studies which must now replace the work of exploration.

It is therefore the purpose of this paper to present only the broadest analysis of the data. Detailed discussion of individual profiles is the function of separate papers, in which preferably groups of profiles from a restricted area should be treated along with those physiographic and historical elements which may account for peculiar differences. Only in this way can a generalized regional profile be prepared, in which edaphic differences are clearly separated from those which are climatic.

The most evident generalization to be drawn from the diagrams is that distinctive regional pollen profiles are a reality. Pollen from remote sources seems within most of the regions studied to be a theoretical, rather than a practical, consideration. It would even be possible to designate regions having characteristic profiles as: $A$, coniferous region, oceanic type, station 1; $B$, coniferous region, continental type, station 19, in the former fir, spruce and birch predominating, in the latter spruce and pine; $C$, humid deciduous forest region, central type, Station 11; $D$, humid deciduous forest region, southern type, Station 6, in the former oak predominating with beech and maple in lesser proportions; in the latter a larger number of genera participating, including notably the gums; $E$, subhumid region, prairie or savannah type, Station 16; $F$, subhumid region, southern forest type, Station 13, in the former the herbaceous pollen predominating, in both the variety of deciduous trees being much less than in $C$ and $D$; and $G$, Rocky Mountain region, Station 20, characterized by conifers and herbs of semi-arid type, with almost complete absence of deciduous forms.

It is to be understood that these distinctions, while real, are purely provisional, to be utilized as scaffolding in the present stage of operations. Gradations are continuous, and the whole business of regional analysis is relative to the refinement of the standards which are proposed (Giles, '30).

A second major generalization appears to be this: The climatic shift accompanying glacial retreat was of a much greater order of magnitude than any fluctuations which have occurred since. No one knows how soon after glacial retreat the longest records (from Ohio, Station 11, Indiana, Station 12, Illinois, Station 15, and Iowa, Station 16) began (Sears, '35). But in each, the shift from a coniferous to the present deciduous or (in Iowa) grassland-savannah vegetation is clearly marked and occurs between the bottom and middle third of the profile.

This affords the basis for Voss' ('34) conclusion that "climatic conditions remained very uniform throughout the period represented by the upper two-thirds of the pollen diagrams." In none of the profiles presented has there been a shift in the upper two-thirds which is equal to the difference between the profiles characteristic of the regions provisionally blocked out in a preceding paragraph. On the other hand, there is considerable evidence of modification during the period thus represented. The regional boundaries have not been static.
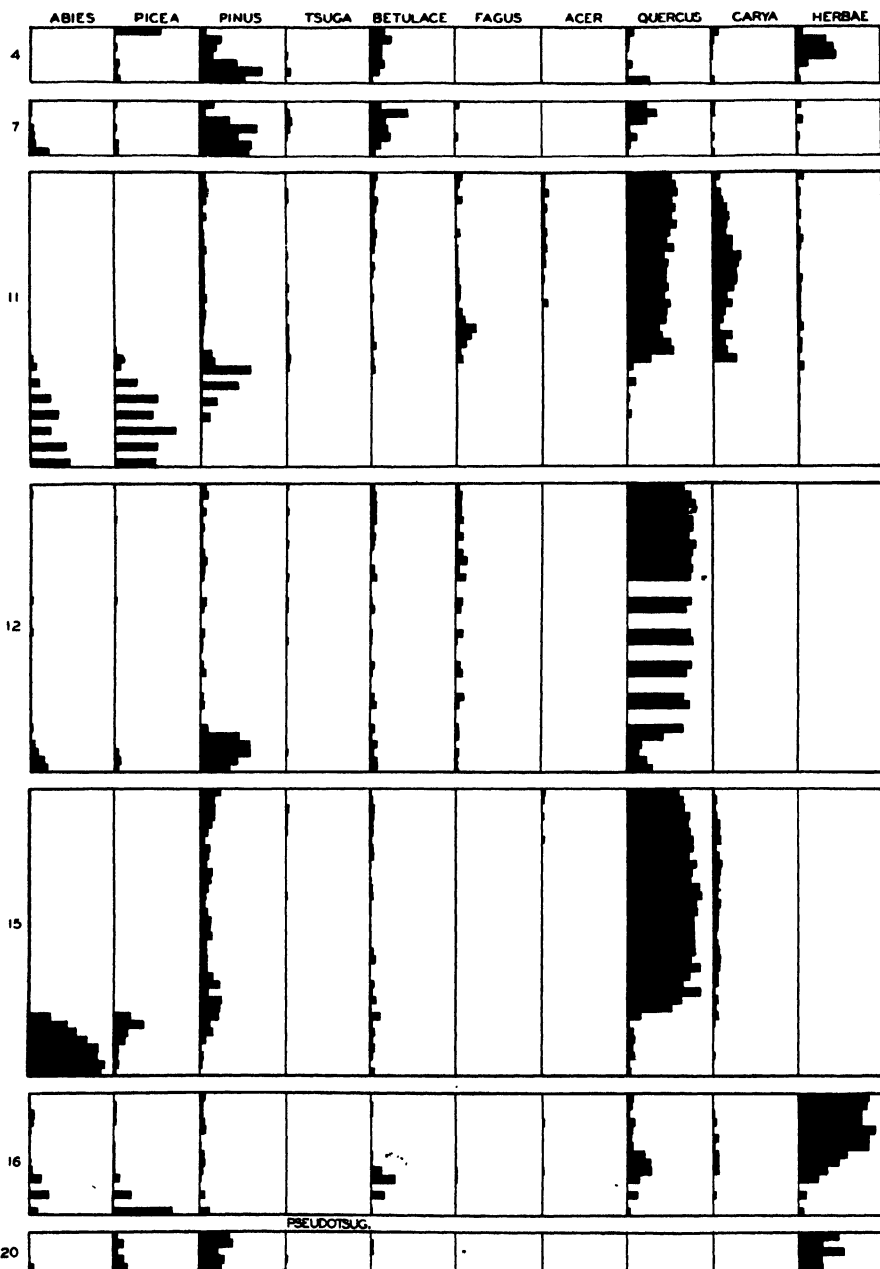
FIG. 7. Comparison of pollen profiles at seven stations ranging from east to west between the 40th and 43d parallels: 4, New Hampshire; 7, Pennsylvania; 11, Ohio; 12, Indiana; 15, Illinois; 16, Iowa; and 20, Wyoming. These illustrate the shift from oceanic to continental conditions in the central deciduous area. Note effect of altitude and longitude in 7 and 20. Postglacial warm dry maximum shown in 11, 15 and 16, although somewhat more diffused than in figure 6 due to generally warmer and drier conditions at this latitude. Transect VI.

This leads to the third major generalization, namely, that the evidence indicates a period of maximum warmth and probably, dryness, now past. This is attested by the maximum of oak at the 17 foot level in IV, Station 10 (Northern Ontario) and its subsequent retreat; by similar conditions at the 18 foot level in IV, Station 19 (Northern Minnesota); at the 14 foot level in III, Station 18 (Central Minnesota); at the 2.5 metre level in II, Station 8 (Welland, Ontario); and is so obvious throughout V as to require no elaboration.

It is further shown by the hickory maximum at the 11 foot level in II, Station 11 (Ohio) and the amaranth-chenopod maximum at the 5 foot level in III, Station 16 (Iowa) but is more diffuse in the central deciduous area than farther north.
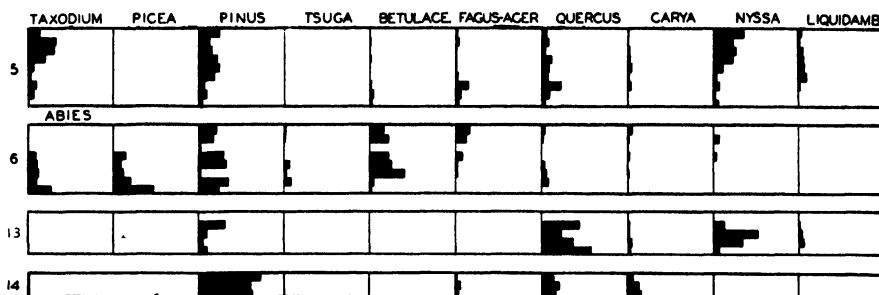


FIG. 8. Comparison of pollen profiles at four stations in the vicinity of the 35th parallel: 5, Virginia; 6, Tennessee; 13, Arkansas; and 14, Oklahoma. Record is short in every case. Chiefly interesting as a study of composition rather than of development. Transect VII.

It is not well shown in the shorter, more recent profiles, nor in those whose record is primarily one of edaphic change. It does not appear clearly in the profile from Illinois (15), nor in those from the same vicinity published with it (Voss '34). This may be due to the buffering of this region by the proximity of Lake Michigan, or to certain technical difficulties in connection with the analysis, as for example the problem of distinguishing between various species of oak.

The post-xerothermic "climatic deterioration," or period of decreasing warmth, is shown best by the general recent increase of spruce at the northern stations. Southward it appears in the form of general evidence of increasing mesophytism—more *Acer*, *Fagus*, *Nyssa*, *Liquidambar*, and southern pine. In fact at the southern stations characteristic austral species generally show a steady increase in the upper levels, suggesting at least that temperature decrease is not yet acting directly in this area, although it may be influencing the relative humidity.

With respect to the transition between early and middle postglacial time, and the bearing of this upon a complete hypothesis, our knowledge is still

insufficient to permit final judgment. The more northerly bogs are too youthful, and in most of those in the central states the record of early post-glacial time is too condensed, if it is present at all. Only the Bucyrus bog shows it *in extenso*, and while it must be admitted that the combined Ohio profile II, Station 11) shows a remarkable correspondence to the Blytt-Sernander sequence it is necessary, for the present, to await more evidence. For a general discussion of this topic the reader may consult Sears ('35).

In the meantime, the simple schedule of von Post ('30)—a period of increasing warmth, period of maximum temperature, period of decreasing warmth—is broad enough to allow of future refinement, and does no violence to the facts. With it as a basis, further work will establish the truth about fluctuations in humidity during the period of rising temperature and so confirm, modify, or eliminate the Blytt-Sernander hypothesis as a principle of wide and general application.

Acknowledgments are due to various colleagues, particularly M. Kaeiser, G. C. Couch and G. Goodman for invaluable help in the preparation of this paper.

## SUMMARY

Pollen profiles of twenty peat deposits widely scattered over eastern North America are arranged in a set of seven transects for graphical comparison.

Distinctive regional characteristics appear, which may be designated tentatively, and merely for present convenience as: *A*, coniferous region, oceanic type; *B*, coniferous region, continental type; *C*, deciduous region, central type; *D*, deciduous region, southern type; *E*, subhumid region, grassland type; *F*, subhumid region, southern forest type; and *G*, Rocky Mountain region.

Fluctuations during the upper two-thirds of the largest profiles have not been as great as the regional differences provisionally noted.

There is rather general evidence of a warm dry climax within the upper two-thirds of the largest profiles, followed by decreased temperature at the north and by increased mesophytism toward the south.

In the absence of sufficient evidence regarding events before the xero-thermic climax the simple hypothesis of von Post, which divides postglacial time into three periods, increasing warmth, maximum temperature, decreasing warmth, fits the facts, and does not exclude later refinements which may develop as the result of more intensive analyses.

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# STUDIES ON VIRGIN HARDWOOD FOREST: III. WARREN'S WOODS, A BEECH-MAPLE CLIMAX FOREST IN BERRIEN COUNTY, MICHIGAN [1]

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Study of the composition of virgin forests in the central states is difficult because of the fragmentary nature of the few remaining tracts and the uncertain knowledge of their historical treatment. Warren's Woods (fig. 1) is reputedly a virgin forest and is held as a state reserve under the Ed-



FIG. 1. A view of Warren's Woods south of the highway showing dominance of beech and the heavy maple understory. Photo by S. A. Cain.

ward K. Warren Foundation of Three Oaks, Berrien County, Michigan. The only recent modification of the area studied, north and west of the Galien River, a small, sluggish stream which penetrates the tract, is that resulting from the removal of dead timber for firewood—a practice of the last four decades. A conversation with an old resident, Mr. Greenberry King, of Three Oaks, who has been in the employ of the owners for several decades,

[1] Contribution No. 69 from the Waterman Institute.

reveals the usual history of old-aged forests which are reputed to be virgin. Mr. King stated that the first cutting of timber in the section was in 1882 and the last in 1891. As the County was established in 1831, it is possible that some selective cutting might have occurred in the half-century or more before Mr. King's acquaintance with the woods.

According to Mr. King, there were two sawmills and a bolt mill operating in the section at one time. The latter cut squares of hard maple and white oak for whipstocks. Earlier operations were mostly in the woods east and south of the river. Later there was some cutting in the portion north and west of the river where the present study was made. The selective cutting in this part took out about 10 per cent of the timber 45 to 50 years ago. The scattered trees removed were basswood, tulip poplar, white oak, and black cherry, and according to Mr. King, would hardly have been missed. No beech, and little maple, was cut. There was no black walnut in the woods. Fifty years ago, as now, the woods was dominantly beech, but not so much so. Mr. King also emphasized the heavy maple reproduction which now attracts so much attention. He remembers this as characteristic since his first acquaintance with the woods. He estimates that in the 50 years or more he has known the woods, probably one-third of the large timber has died, blown down, and been removed for firewood. At no time was any very large timber in the woods. He recalls one white oak about 3 feet on the stump. The black cherry removed ran 12 to 14 inches on the stump, the white oak, 18 to 20 inches, and one maple was about four feet.

Perhaps the most outstanding features of the woods are the high dominance of beech, the heavy maple reproduction up to about 3 inches d.b.h., the absence of pole trees of maple, and a scattering of old standard maples. The flora of the woods as a whole is very rich (Billington, '24), but in the virgin portion the herbaceous layer is very open, as is the shrub layer, due to the density of the crown, and arborescent reproduction.

The climate of this region is marked by long, cold winters, and pleasant summers, both seasons being modified by proximity to Lake Michigan. The region has about 180 days growing period and between 32 and 36 inches rainfall, evenly distributed through the year. The mean annual rainfall is 31.11 inches; known extremes are 45.12 inches in 1902, and 22.82 inches in 1913. The average snow is 51.6 inches, more than half of which falls in January and February.

The woodland tract studied lies wholly in the Nappanee silt loam soil type, Kerr, et al. ('27), in the NW. ¼, Sec. 27, R. 20 w., Twp. 7 S. The Nappanee loams are partly wind deposited and are also characterized by heavy, mottled, gray and yellow subsoil. The surface drainage is good but the underdrainage is poor.

## RESULTS OF THE QUADRAT SURVEY

In the summer of 1933, 25 quadrats, 10 by 10 meters, were scattered regularly in a checkerboard pattern over a little more than 10 acres of the upland area south of the highway and north of the Galien River. Thirty meters intervened between the quadrats giving a sampling of about 6 per cent. Table I gives the density and frequency data for the woody species

TABLE I. *Density and frequency of woody plants of Warren's Woods, based on 25 quadrats each 10 by 10 meters*

| Species and layers | Under 1 ft. high | | Over 1 ft. & under 1 in. d.b.h. | | 1 in. d.b.h. and over | | Total | |
|---|---|---|---|---|---|---|---|---|
| | D | F % | D | F % | D | F % | D | F % |
| A. Superior arborescent layer | | | | | | | | |
| *Acer rubrum* | 132 | 40 | 14 | 20 | 5 | 20 | 151 | 52 |
| *A. saccharum* | 3,923 | 100 | 1,055 | 100 | 82 | 92 | 5,060 | 100 |
| *Carya cordiformis* | 38 | 60 | 3 | 12 | 1 | 4 | 42 | 64 |
| *C. ovata* | 1 | 4 | 1 | 4 | 3 | 12 | 5 | 20 |
| *Celtis occidentalis* | 1 | 4 | 0 | 0 | 0 | 0 | 1 | 4 |
| *Fagus grandifolia* | 156 | 80 | 230 | 100 | 97 | 100 | 483 | 100 |
| *Fraxinus americana* | 105 | 56 | 30 | 44 | 2 | 8 | 137 | 64 |
| *Liriodendron Tulipifera* | 7 | 24 | 2 | 4 | 2 | 4 | 11 | 24 |
| *Prunus serotina* | 69 | 40 | 9 | 16 | 6 | 20 | 84 | 44 |
| *Quercus alba* | 4 | 8 | 1 | 4 | 0 | 0 | 5 | 8 |
| *Q. borealis* var. *maxima* | 52 | 56 | 4 | 16 | 4 | 8 | 60 | 64 |
| *Tilia glabra* | 31 | 28 | 8 | 20 | 3 | 12 | 42 | 40 |
| *Ulmus americana* | 235 | 60 | 3 | 12 | 6 | 20 | 244 | 64 |
| *U. fulva* | 1 | 4 | 2 | 8 | 2 | 8 | 5 | 16 |
| B. Inferior arborescent layer | | | | | | | | |
| *Amelanchier laevis* | 9 | 4 | 1 | 4 | 1 | 4 | 11 | 8 |
| *Asimina triloba* | 3 | 12 | 7 | 12 | 0 | 0 | 10 | 16 |
| *Carpinus caroliniana* | 75 | 48 | 53 | 68 | 25 | 52 | 153 | 76 |
| *Cornus florida* | 7 | 8 | 3 | 8 | 0 | 0 | 10 | 8 |
| *Ostrya virginiana* | 22 | 16 | 18 | 40 | 23 | 48 | 63 | 60 |
| *Prunus americana* | 29 | 12 | 21 | 4 | 1 | 4 | 51 | 16 |
| C. Tall shrub layer | | | | | | | | |
| *Hamamelis virginiana* | 11 | 20 | 30 | 36 | 5 | 16 | 46 | 40 |
| *Benzoin aestivale* | 713 | 92 | 732 | 88 | 3 | 8 | 1,448 | 96 |
| D. Shrub layer | | | | | | | | |
| *Dirca palustris* | 0 | 0 | 6 | 12 | 0 | 0 | 6 | 12 |
| *Grossularia Cynosbati* | 24 | 24 | 5 | 8 | 0 | 0 | 29 | 24 |
| *Lonicera canadensis* | 41 | 24 | 9 | 12 | 0 | 0 | 50 | 28 |
| *Sambucus canadensis* | 4 | 16 | 1 | 4 | 0 | 0 | 5 | 16 |
| *S. pubens* | 0 | 0 | 8 | 12 | 0 | 0 | 8 | 12 |
| *Smilax rotundifolia* | 15 | 20 | 0 | 0 | 0 | 0 | 15 | 20 |
| *Viburnum acerifolium* | 217 | 32 | 180 | 40 | 0 | 0 | 397 | 48 |
| *V. affine* | 0 | 0 | 1 | 4 | 0 | 0 | 1 | 4 |
| Total density (2,500 sq. m.) | 5,925 | | 2,437 | | 271 | | 8,633 | |

encountered in the quadrats, by three size classes: (1) under one foot high; (2) between a foot high and under one inch d.b.h.[2]; (3) one inch d.b.h. or over.

[2] Diameter breast high.

Of the tree reproduction less than one foot high, *Acer saccharum*,[3] with 3,923 plants (for the area sampled, 2,500 sq. m.), far outnumbers all other species, in fact it has a higher density than all the other species together. *Ulmus americana* is second, with 235 plants, but they are nearly all first-year seedlings. Three species form the next group: *Fagus grandifolia* (156 plants), *Acer rubrum* (132 plants), and *Fraxinus americana* (105 plants). Of the species which attain the upper canopy on maturity, only *Prunus serotina* and *Quercus borealis* var. *maxima*, in addition to the above, have any fair representation. Among the shrubs, *Benzoin aestivale* is also in a group by itself, with 713 plants. In addition, only *Viburnum acerifolium* is conspicuous. Woody plants sometimes form a high cover on the forest floor. These were not counted, but were mostly *Parthenocissus quinquefolia, Rhus toxicodendron*, and *Evonymus obovatus*.

The next group, containing plants up to one inch d.b.h., is still dominated by *Acer saccharum*, with 1,055 stems, although the proportion to *Fagus grandifolia* is less than in the smaller size group. In the third size group, from one inch d.b.h. up, *Acer* and *Fagus* are nearly equal in numbers, with 82 and 97 respectively. However, there is a great difference between these two species in their size distribution, table II. In the one, two, and three inch

TABLE II. *Distribution through diameter classes, and the basal area of the trees of Warren's Woods, 25 quadrats 10 by 10 meters*

| Species | Diameter breast high in inches | | | | | | | | | | | | Total | Basal area in sq. ft. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7–12 | 13–18 | 19–24 | 25–30 | 31–36 | 60 | | |
| **A.** | | | | | | | | | | | | | | |
| *Acer rubrum* | 2 | | | | | | 1 | | | | 2 | | 5 | 14.0 |
| *A. saccharum* | 61 | 12 | 3 | 1 | 1 | | | | 2 | 1 | 1 | | 82 | 16.7 |
| *Fagus grandifolia* | 38 | 8 | 1 | 3 | | 2 | 14 | 15 | 14 | 2 | | | 97 | 70.5 |
| *Fraxinus americana* | 1 | | | | | | 1 | | | | | | 2 | .5 |
| *Prunus serotina* | 2 | 1 | | | | | 3 | | | | | | 6 | 1.7 |
| *Quercus borealis maxima* | | | | | | | 2 | | 1 | 1 | | | 4 | 7.5 |
| *Tilia glabra* | | 1 | 1 | 1 | | | | | | | . | | 3 | .2 |
| *Ulmus americana* | 2 | | 1 | | | | | | 1 | 1 | | 1 | 6 | 27.4 |
| **B.** | | | | | | | | | | | | | | |
| *Carpinus caroliniana* | 14 | 6 | 4 | 1 | | | | | | | | | 25 | .5 |
| *Ostrya virginiana* | 12 | 7 | 3 | 1 | | | | | | | | | 23 | .3 |

Total (2,500 sq. m.) ............................................. 253   139.3
Total (per acre) ................................................ 365   223

Other species of less than 0.1 sq. ft. basal area are: *Amelanchier laevis, Carya cordiformis, Carya ovata, Liriodendron tulipifera, Prunus americana, Ulmus fulva, Hamamelis virginiana,* and *Benzoin aestivalis.*

[3] Nomenclature follows Deam ('32a and b).

TABLE III. *Frequency percentage of herbaceous species of Warren's Woods compared with Billington's ('24) abundance designations, same woods*

| Species | Frequency per cent | Billington's abundance designations [1] |
|---|---|---|
| **Ferns** | | |
| *Aspidium noveboracense* (L.) Sw. | 16 | *a* |
| *A. spinulosum* var. *intermedium* (Muhl.) D.C.E. | 64 | *a* |
| *Adiantum pedatum* L. | 8 | *o* |
| *Asplenium filix-femina* (L.) Bernh. | 8 | – |
| *Onoclea sensibilis* L. | 4 | – |
| *Osmunda claytoniana* L. | 4 | *f* |
| *Polystichum acrostichoides* (Michx.) Sch. | 20 | *f* |
| **Grasses and sedges** | | |
| *Brachyelytrum erectum* (Schreber) Beauv. | 4 | *f* |
| *Glyceria nervata* (Willd.) Trin. | 8 | *a* |
| *Hysterix patula* Moench. | 8 | *o* |
| *Carex grayii* Carey | 4 | *f* |
| *C. laxiflora* Lam. | 12 | *f* |
| *C. pennsylvanica* var. *leucorum* (Willd.) Fern. | 20 | *a* |
| *C. plantaginea* Lam. | 56 | *f* |
| *C. spp.* | 20 | – |
| **Other herbs** | | |
| *Actea alba* (L.) Mill. | 16 | *o* |
| *Arisaema triphyllum* (L.) Schott. | 64 | *f* |
| *Boehmeria cylindrica* (L.) Sw. | 4 | *f* |
| *Caulophyllum thalictroides* (L.) Michx. | 20 | *f* |
| *Circaea alpina* L. | 4 | – |
| *C. luteliana* L. | 20 | *f* |
| *Dentaria maxima* Nutt. | 4 | – |
| *Dioscorea villosa* L. | 4 | – |
| *Epifagus virginiana* (L.) Bart. | 16 | *a* |
| *Galium aparine* Michx. | 56 | *a* |
| *G. circaezans* Michx. | 4 | *f* |
| *G. concinnum* T. & G. | 16 | *f* |
| *G. triflorum* Michx. | 4 | *f* |
| *Geranium maculatum* L. | 4 | *a* |
| *Geum canadense* Jacq. | 8 | *o* |
| *Hepatica acutiloba* D.C. | 4 | *a* |
| *Impatiens pallida* Nutt. | 8 | *a* |
| *Laportea canadensis* (L.) Gaud. | 4 | *f* |
| *Maianthemum canadense* Desf. | 16 | *a* |
| *Mitchella repens* L. | 4 | *f* |
| *Osmorhiza claytoni* (Michx.) Clarke | 20 | *a* |
| *Phytolacca decandra* L. | 4 | *o* |
| *Pilea pumila* (L.) Gray | 4 | – |
| *Polygonatum biflorum* (Walt.) Ell. | 12 | *a* |
| *Polygonum virginianum* L. | 12 | – |
| *Ranunculus abortivus* L. | 8 | *f* |
| *Smilacina racemosa* (L.) Desf. | 36 | *a* |
| *Solidago caesia* var. *axillaris* (Pursh.) Gray | 4 | *a* |
| *Trillium grandiflorum* (Michx.) Salisb. | 4 | *f* |
| *Viola canadensis* L. | 8 | *a* |
| *V. papilionacea* Pursh. | 20 | *f* |
| *V. scabriuscula* Schwein. | 4 | *a* |
| *V. striata* Ait. | 4 | *a* |

| Total, 48 species | Raunkiaer's F-classes | | Billington's abundance classes | |
|---|---|---|---|---|
| | A ( 1– 20%) | 43 spp. | – | 8 spp. |
| | B (21– 40%) | 1 sp. | *o* | 5 spp. |
| | C (41– 60%) | 2 spp. | *f* | 18 spp. |
| | D (61– 80%) | 2 spp. | *a* | 17 spp. |
| | E (81–100%) | 0 | | |

[1] *o* means occasional; *f* means frequent; *a* means abundant.

d.b.h. classes, *Acer* surpasses *Fagus*. Above that dimension for *Acer* there was only one-tree each of 4 and 5 inches d.b.h., and none other on all of the quadrats to about the two-foot class. The present dominance of *Fagus* is apparent from its basal area of 70.5 square feet (112.8 sq. ft. per acre) for the area sampled, compared with *Acer* at 16.7 square feet (26.7 sq. ft. per acre). Species represented by a scattering of older trees, and with sufficient reproduction to maintain their rôle in the forest, although a minor one, are *Ulmus americana, Acer rubrum,* and *Quercus borealis* var. *maxima*.

Frequency percentages, table I, give some indication of the evenness of distribution of the wooody species on the 25 quadrats. *Acer* and *Fagus* are both of 80 per cent or more frequency through the size groups. No other tree species of the superior arborescent layer has a frequency above class *B* (21 to 40 per cent) except *Fraxinus americana* for reproduction under one inch d.b.h. and *Carya cordiformis, Ulmus americana,* and *Quercus borealis* var. *maxima,* for reproduction under one foot high. The small trees, *Carpinus* and *Ostrya,* attain a frequency in class *C*. Among the shrubs, only *Benzoin* falls in class *E,* while *Viburnum acerifolium* reaches class *C,* with a total of 48 per cent. The individual frequencies for the woody species of all sizes when summarized by Raunkiaer's classes give the following results: Class *A,* 43; *B,* 20; *C,* 9; *D,* 14; and E, 14 per cent.

Table III gives the frequency of 48 herbaceous species found on the quadrats together with Billington's ('24) abundance designations. The heterogeneity and discontinuity of the herbaceous layer is well illustrated by the fact that 43 of the 48 species fall in class *A,* being present in only 1 to 5 out of the 25 quadrats. This is especially significant in view of the large size of the quadrats and emphasizes the open nature of the herbaceous layer. Those species in excess of 20 per cent frequency are: *Aspidium spinulosum* var. *intermedium* (64), *Carex plantaginea* (56), *Arisaema triphyllum* (64), *Galium aparine* (56), and *Smilacina racemosa* (36).

Figure 2 gives coverage data for the natural layers of the woods. The superior arborescent layer, which ranges over 100 feet in height, is uniformly of high coverage, class 5 (76–100 per cent). A fallen beech tree measured 17.5 inches d.b.h., 45 feet to the first limb, and 108 feet high. Nearby, but not in any quadrat, stood a red oak of 49 inches d.b.h. The inferior arborescent layer, exclusive of transgressives of the superior layer, does not average over class 1 (1–5 per cent), although in patches *Carpinus* and *Ostrya* total in class 2 or 3. The tall shrub layer averages in class 2 (6–25 per cent), with *Benzoin* the principal member, frequently in class 3 (26–50 per cent), and sometimes as high as class 5. In six quadrats *Acer* reproduction attained a coverage in class 4 (51–75 per cent) in this layer. Looking·through the woods as a whole, *Acer* reproduction frequently forms a story 12–15 feet high (fig. 1). The low shrub layer does not average more than class 1 although in places it runs as high as class 2 or 3 due to the local abundance of *Parthenocissus* and *Rhus*. The herb layer is usually of low coverage and

nowhere exceeds 25 per cent. The shade, and especially the competition of *Acer* reproduction and local alternating patches of *Benzoin* in low places, are responsible for the low coverage of the herbs and small shrubs. The *Parthenocissus* layer is about the same height as the herb layer. These groups commingle, or form a mosaic of variable coverage.
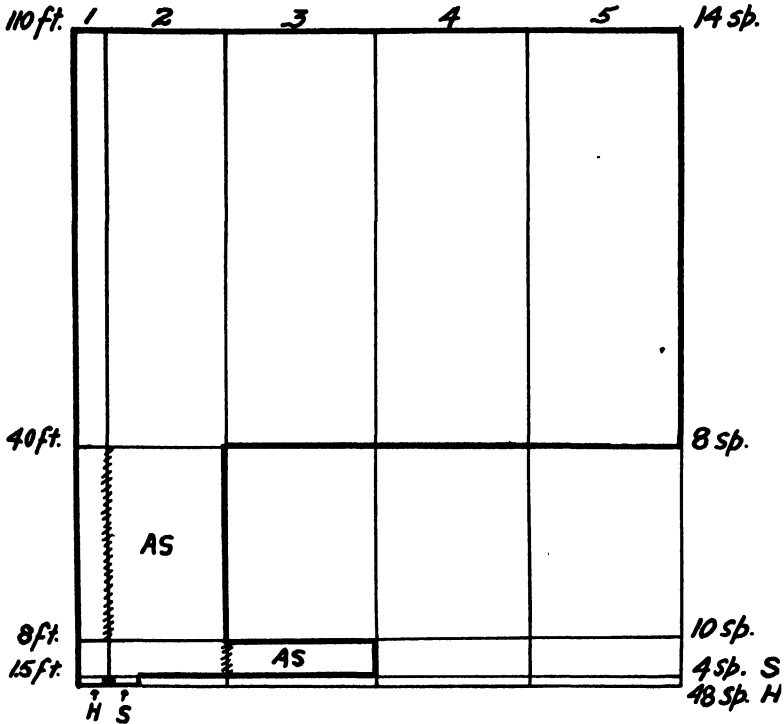


Fig. 2. A coverage-stratification diagram of Warren's Woods. The vertical columns represent the five coverage classes in percentage. The horizontal columns represent the natural layers of the vegetation. The heavy line shows the coverage in each layer. *H* and *S* indicate the herbaceous layer and the low shrub layer which are of about the same height. The coverage in each inferior layer (by the plants which form the natural layer) is augmented by transgressives, in this case, principally reproduction of *Acer saccharum* (AS). The number of species in each layer, as ascertained by the quadrat survey, is given at the right.

If statistics for the inferior layers had been based on smaller quadrats, located only where the particular layers were present rather than at stated intervals, they would, of course, be vastly different. Perhaps that method would have been better for it would have revealed the rôles of the herbs and shrubs within their restricted areas. The present system, however, gives a truer picture of the relationship of these communities to the whole area of the woods.

In looking over quantitative studies one is likely to place too great faith

in the numerical values given for the species. It must be kept in mind that they are derived from sampling and that for the less frequent and abundant species especially the numerical values have a high probable error. Also, the relationships revealed depend to some extent on the size and number of
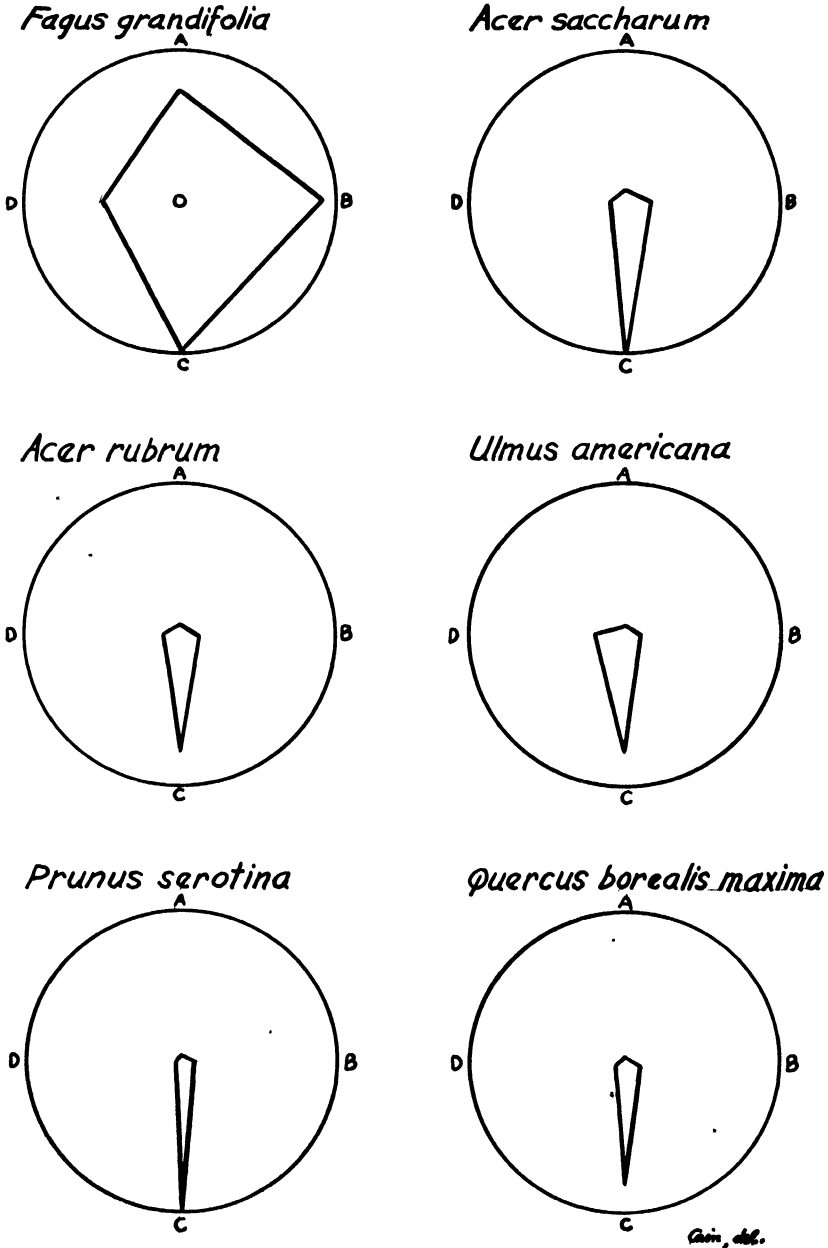


FIG. 3. Lutz phytographs for the six leading tree species.

the sample areas. It is firmly believed, however, that such quantitative studies are of much greater value in community study than the best general descriptions, and that the true rôles of the species, especially those of high and of low value, can be closely approximated by the quadrat method.

Lutz ('30), in a study of a virgin forest tract in northwestern Pennsylvania, has developed the phytograph, a valuable graphic method of portraying the relative importance of different species. Data for the construction of phytographs for the six leading tree species of Warren's Woods are given in table IV.

TABLE IV. *Data for the construction of the phytographs, Warren's Woods*

| Species | Abundance per cent [1] | Frequence per cent [2] | Size classes and per cent [3] | Basal area in sq. ft. and per cent [4] |
|---|---|---|---|---|
| *Fagus grandifolia* | 39 (74) | 88 (100) | 5 (100) | 70.5 (50) |
| *Acer saccharum* | 4 (7.5) | 16 (92) | 5 (100) | 16.7 (12) |
| *Acer rubrum* | 3 (5.6) | 12 (20) | 4 (80) | 14.0 (10) |
| *Ulmus americana* | 3 (5.6) | 8 (20) | 4 (80) | 27.4 (20) |
| *Prunus serotina* | 2 (3.8) | 8 (20) | 5 (100) | 1.7 (2) |
| *Quercus borealis* var. *maxima* | 2 (3.8) | 8 (8) | 4 (80) | 7.5 (5) |
| 12 other species | none | none | 6 (60) | 1.7 (2) |

[1] Radius AO: Abundance and per cent of total abundance of stems 10 in. d.b.h. or over.
[2] Radius BO: Frequency per cent of trees 10 in. d.b.h. or over: (in parentheses, F–% of stems 1 in. d.b.h. or over).
[3] Radius CO: Number and per cent of size classes in which species are found. The classes are: under 1 ft. high, over 1 ft. high and under 1 in. d.b.h., 1 to 3 in. d.b.h., 4 to 9 in. d.b.h., 10 in. d.b.h. and over.
[4] Basal area in sq. ft. and per cent of total basal area.

## DISCUSSION

It is worth calling attention to three outstanding papers on the northern hardwood forest as a whole: Frothingham ('15), Zon and Garner ('30), and Dana ('30). Some papers giving considerable quantitative data on the beech-maple climax forest in Michigan are by Clayberg ('20), Quick ('23), Gleason ('24), Wollett and Sigler ('28), and McIntire ('31). There are a few papers dealing with the type or associated types and variants in other localities as, for example, Bergman ('23) for Minnesota, Jennings ('27) and Illick and Frontz ('28) for Pennsylvania, Esten ('32) for Indiana, but as has already been stated, exact information is lacking except for a few more or less isolated situations. Also, one finds an attempt to synthesize the various quantitative data largely thwarted because of diverse sampling methods which prevent the resulting data from being directly comparable. Recently the writer (Cain '32a) has presented a brief discussion of certain concepts well-established in European plant sociology (Braun-Blanquet '32) and has been attempting to apply some of these principles to virgin hardwood forests in the Central States (Cain '32b and '34).

Frothingham ('15) points out the distinction between the northern and the southern hardwood forests. Several important species are found in both. The northern hardwood forest is distinguished by the presence of yellow birch, white pine, and eastern hemlock, and the absence of yellow poplar, red gum, sycamore, and several other more southern species. The northern hardwood forest, with about 21 important hardwoods, is much simpler in composition than the southern, which has fully 95 species of local or general commercial value, according to Frothingham. The northern hardwood forest is divided into two regions: the Eastern Mountain region and the Great Lakes region. The latter is generally in the area of the Wisconsin glaciation. Regional variations in the composition of the forest are induced by the varying response of the individual species to rainfall diminution westward and southward, and to temperature diminution northward and with altitude. Locally over the region any one, a few, or several species may be dominent. In the Lake States there is usually an abundance of basswood and elm which forms the most striking general distinguishing characteristic of the northern hardwoods there. Westward the beech drops out first and then the hard maple becomes of less importance.

McIntire ('31) has shown that basswood and elm are not uniformly characteristic of the Lake States hardwood type group. He has published a sound discussion of theory and practice of forest typing as a result of the field experience of the Michigan Land Economic Survey. The Survey finally recognized in Upper Michigan four distinct upland hardwood types: *Type M*—Hard maple-beech-elm-basswood-yellow birch, *Type Mb*—Hard maple-beech-yellow birch, *Type Mc*—Hard maple-elm-basswood-yellow birch, *Type My*—Hard maple-yellow birch, hard maple usually ranking first and yellow birch last.

Quick ('23), discussing the varying composition of the climax forest in southern Michigan, says that *Acer saccharum* and *Fagus grandifolia* are found all over the area but are about twice as frequent on clay as on sandy soils. *Carya cordiformis, Tilia glabra, Liriodendron tulipifera, Nyssa sylvatica*, and *Ostrya virginiana* are more frequent southward while *Betula lutea* and *Fraxinus nigra* are more frequent northward.

. For the state as a whole we can figure the following percentages from data given by Frothingham ('15), who takes his information from a survey of privately owned timber in 1913: Maple 50 per cent, birch 20, basswood 8, elm 8, beech 6, and miscellaneous 8 per cent. The northern hardwood forest, as extensive and rich in species as it is, naturally forms a great many forest types. The forest cover type report of the Society of American Foresters ('32) gives a classification of hardwood forest types with which we are interested in allocating Warren's Woods to its proper position. Although Warren's Woods is definitely dominated by beech, figure 3 and table II, it cannot be summarily assigned to their Type 58—Beech, which is described as, " Type created and extended by cutting through northern and eastern Ohio into

central Indiana. Common in ' flats ' of Indiana and along all stream courses of mountain and hill region where heavy soils are poorly drained. . . . Widely distributed most common single species type in Ohio and Indiana." Type 57—Beech-sugar maple, fits our situation much better, although sugar maple does not yet play a sufficient rôle in the dominant tree class. This type is described from the Ohio Valley and southern Michigan with red maple, white oak, red oak, hemlock, red elm, American elm, basswood, pignut, shagbark and mockernut histories, and black cherry as associates, occurring on fresh soils.

The absence of yellow birch and hemlock from the forest, the absence of maple codominance, and the unimportance of basswood and elm prevent this woods from being classified under any of the northern forest types. Neither is Warren's Woods of the southern hardwood forest in the sense of Frothing- ham, but it falls closest to Type 57—Beech-sugar maple, of the central forest, although as pointed out, sugar maple is now distinctly unimportant except for reproduction up to three inches d.b.h. It should also be remembered that Mr. King described the selective cutting of a little white.oak, basswood, and black cherry which are associates of beech and maple in Type 57.

Wollett and Sigler ('28), in a study of revegetation of beech-maple areas in the Douglas Lake region of Michigan, note the following interesting con- trasts between beech and maple: In the typical old-aged beech-maple forests, beech 21.2 per cent and maple 35.9 per cent. In the reforesting areas, beech 6.8 per cent and maple 67.3 per cent. Sugar maple is the most agressive re- producer throughout the characteristic beech-birch-maple region in old-aged woods as well as in revegetating areas. Beech, which is probably more toler- ant, does not bear large seed crops annually and much is destroyed by ani- mals.[4] It would appear that the balance will be in favor of sugar maple as time goes on and that the tract will approach closer to a codominance of maple with beech, as is more common farther north. The conspicuous gap in sugar maple trees between 6 and 22 inches d.b.h. may be attributable to some cutting of maple of which we have no record.

Frothingham ('15) gives the following approximate average age-diameter classes for sugar maple in Michigan and vicinity: 50 years old, 2.7 inches d.b.h.; 100 years old, 7.0 inches; 150 years old, 11.9 inches; 200 years old, 16.7 inches, and 250 years old, 21.1 inches. Gates and Nichols ('30) found that sugar maple in primeval forests of Michigan has the following age-diameter distributions: 1–4 inches d.b.h. were 33.3 per cent of 1–50 years and 66.7 per cent of 51–100 years. At the other limit of the gap in diameter dis- tribution for maple in Warren's Woods their data is again of interest: 21–24 inches d.b.h., trees were 44 per cent of 101–150 years old, 20 per cent of 151– 200 years, 24 per cent of 201–250 years, and 12 per cent of 251–300 years. As already suggested, this may be interpreted to mean that in Warren's Woods,

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[4] It is of interest to call attention to a paper by Dice ('20) on the mammals of War- ren's Woods.

some 50 years ago or more, hard maple trees from about 4 to 20 inches d.b.h. were cut for use by the wood-working factory, although no records exist to show this.

Another possible explanation of the absence of pole trees of sugar maple in Warren's Woods may be that of a very high mortality of middle-aged maple trees. The old maples which are present would have to have attained codominance with the beech many decades ago. At the present time the contrast of beech and maple for the different size groups is as follows:

| Size groups | Density Beech | Maple | Ratio |
|---|---|---|---|
| Under 1 foot high | 156 | 3,923 | 1 to 25 |
| Under 1 inch d.b.h. (Over 1 foot high) | 230 | 1,055 | 1 to 4 |
| 1 inch d.b.h. | 38 | 61 | 1 to 2 |
| 2 inches d.b.h. | 8 | 12 | 1 to 1.5 |
| 3 inches d.b.h. | 1 | 3 | 1 to 3 |
| 4–9 inches d.b.h. | 11 | 2 | 5.5 to 1 |
| 10 inches d.b.h. or over | 39 | 4 | 10 to 1 |
| Basal area (2,500 sq. m.) | 70.5 sq. ft. | 16.7 sq. ft. | 4 to 1 |

Esten ('32), studying a beech-maple woods in west-central Indiana, from which large maples were absent, records the following data which is more or less parallel to the above:

| | Beech | Maple | Ratio |
|---|---|---|---|
| Under 2 inches d.b.h. | 224 | 3,392 | 1 to 14 |
| 2 inches d.b.h. | 10 | 23 | 1 to 2.3 |
| 4 inches d.b.h. | 3 | 12 | 1 to 4 |
| 6 inches d.b.h. or over | 24 | 2 | 12 to 1 |
| Basal area (2,500 sq. m.) | 41.7 sq. ft. | 2.7 sq. ft. | 15 to 1 |

Since, as was mentioned in the introduction, it has been the practice for some forty years to remove all dead and fallen trees (and only those), it may be that among those maple predominated. Such a situation would require a considerably higher mortality of middle-aged maple than beech and there seems to be no immediate evidence for this assumption.

Another possible explanation of the size distributions of beech and maple in this woods and elsewhere and especially of the differential reproductive rates and survival rates may lie in recent climatic changes. That is, beech, which is at its western limit in the vicinity of Warren's Woods and in central-western Indiana, may be undergoing some slow change, either as to its geographical limits or vitality.

A final suggestion, and one which has considerable probability, is that clearing off the timber of most of the surrounding land for agricultural purposes during the last 50 to 100 years has resulted in a lowering of the water-table. This, in turn, would result in throwing the balance in favor of maple reproduction rather than beech reproduction.

It is recognized that none of these suggestions is as yet proven although each is more or less tenable. Despite the indications mentioned above, it does not seem to the writer that we are yet justified in saying that maple is gen-

erally tending to increase in importance over beech in these western areas now dominated by beech, but this successional tendency is strongly indicated for several places known to the writer in Indiana and Michigan.

The writer recognizes gratefully the assistance of Mr. Richard Schweers, of Indiana University, who helped him obtain much of the field data. Recognition and appreciation are given the Waterman Institute, Indiana University, which has retained the writer as an Associate since June, 1933.

## SUMMARY AND CONCLUSIONS

1. Data, obtained from 25 quadrats each 100 sq. m., are presented on the composition of an old-aged beech-maple forest in southwestern Michigan. These data include density and frequency of woody plants by size groups, frequency of herbaceous species, and coverage in the natural layers of the forest community. The relative importance of certain tree species is shown by Lutz phytographs.

2. The beech-maple and related forest types are discussed in the light of the literature on the region with the conclusion that Warren's Woods fits most closely to Type 57 of the Society of American Foresters, although the present percentage of dominant maple is very low.

3. Some data are presented on the relative importance of beech and maple of the different size groups and the possible significance of the abundant maple reproduction as to successional trends, with the tentative conclusion that maple seems destined to increase in importance.

4. The effect of selective cutting, in some cases so many decades ago that exact information is unattainable, on the simplification of the existing cover type is discussed with the obvious conclusion that even in reputedly virgin forests one has to advance with caution in considering forest type affinities. It is also obvious that the only practical solution of the forest type problem, when typing is based on the tree layer alone as is the American practice, is that which is based on the existing tree stand, although past treatment and successional trends are of great interest.

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# THE UNDIFFERENTIATED DECIDUOUS FOREST CLIMAX AND THE ASSOCIATION-SEGREGATE

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Conditions in the deciduous forest south of the glacial boundary have long been recognized as far more complex than those in the younger areas to the north of that boundary. Developmental or dynamic ecology, both in America and Europe, has largely grown up in these younger areas; itś terminology is well suited to these simpler conditions. But for the more complex forests of the southern Appalachian region, and other comparable areas, it is inadequate.

The writer recognizes the multiplicity of terms already in use and the almost hopeless confusion surrounding some of them. It may therefore appear inadvisable to some to introduce an additional term; this however seems mandatory from recent studies in the deciduous forest. The term proposed is *association-segregate*. The association-segregate is a climax unit.

As an example of the application of the term *association-segregate* let us consider the mixed mesophytic forest. The term "mixed mesophytic forest" has been used by a number of writers (Transeau, '27; Sampson, '30, Gordon, '32; Braun, '16) to designate an association of the deciduous forest in which a number of species share dominance. Toward the limits of the geographic range of this association, for example in southern Ohio, the mixed mesophytic forest is usually one in which beech, sugar maple, tulip, buckeye, basswood and white ash are important more or less co-dominant species. Variants (toward the limits of geographic range) are introduced by the dropping out of one or more of these species, not usually by any pronounced regrouping. Such is not the case farther south in the area of maximum development of the mixed mesophytic forest. There, variety in expression, due to segregation and regrouping of the dominants, results in many, at first sight entirely unlike, communities with different dominants. In one area (Pine Mountain in the Cumberland Mountains) seven distinct segregates are recognizable (Braun, '35). Each of these would be termed an association-segregate.

Let us now analyze the situation over a period of time, so that a time-space correlation can be made. No consideration of eastern deciduous forest can ignore the conditions of the Tertiary. Fossil evidence is sufficient to prove the great extent of a mixed hardwood forest, the original undifferentiated climax, in North America, Europe and Asia, a hardwood forest so uniform throughout its north-temperate range that it was marked

throughout by the same genera and to some extent species.    This mixed forest was the panclimax of the Tertiary.

Under stress of changing climates the extent of forest was lessened.    A certain segregation of northern and southern types became evident in the Pliocene.    In North America shrinkage from the west due to increasing aridity of the interior, coincident upon the rising Rocky Mountains resulted in segregation of communities on a basis of moisture requirements of their constituent species, and retreat eastward of those of highest demands. Many relics to the west of the Mississippi attest this fact (Clements, '34). Glaciation in the north resulted in a southward crowding of the temperature belts of vegetation, and, particularly, in the destruction of all vegetation over the vast glaciated territory.    These movements were not contemporaneous; neither is the order in which they occurred of great importance. Lesser climatic oscillations of post-Pleistocene time have been contributory, but the two great movements remain, the original shrinkage of deciduous forest away from the interior and its retreat from and elimination in the north.    The result of the first great movement was: (1) the retreat of the most mesophytic species from the western portion of deciduous forest and the consequent increased dominance of species of lesser moisture requirements, establishing there the prevalence of the oak-hickory type, an association-segregate of the original mixed hardwood forest; and (2) the localization in the Appalachian mountain and plateau region of the mixed forest of the Tertiary. This was not disturbed in the southern Appalachian region, at least not greatly, by the southward migrations of the Pleistocene.    It then served as a center of dispersal northward and of repopulation of the denuded glaciated territory as was recognized by Adams ('03).

What has happened or is happening in the stronghold of the mixed forest today?    It has segregated into a large number of communities.    (The large number of types recognizable is demonstrated by such lists as that prepared by the Society of American Foresters, 1932.)    Those which are climax communities (climatic climax) are mesophytic and constitute the mixed mesophytic forest association represented by a large number of association-segregates; those of lesser moisture requirements, as oak-chestnut, are subclimax communities, physiographic climaxes on dry slopes and ridges (Braun, '35).    Within the undifferentiated climax area the various association-segregates bear a relation to one another which is proportionate to the degree of mesophytism of the habitat    These association-segregates are expressions of the mixed climax which are called forth by conditions of the environment.    When and where these conditions become the climatic conditions, the association-segregate becomes the climax association of the region.    The association-segregate of one geographic or climatic unit area may become the association of another slightly different climatic area.    Each of the deciduous forest (climax) associations bears this relation to the mixed or undifferentiated climax.    However, only a few of the association-segregates

of the mixed forest are represented by climax associations outside of the area of the undifferentiated climax. If this derivation of association from association-segregate be recognized, the puzzling juxtaposition of two different apparent climax communities in the same geographic area is more readily explained.

The gradation in dominance and diminution in number of association-segregates from a center outward is demonstrable by a comparison of forest composition in different parts of the deciduous forest. This statement is based on a study now in progress of forest types of the deciduous forest—association-segregates and associations—with a view to the analysis of deciduous forest climaxes.

Segregation may be brought about by the retreat of certain species and persistence of others, those persisting constituting a segregate. This happens with decreasing moisture. When this is local the community may be considered subclimax; when it becomes regional the community is a true climax or climatic climax. In this way, the oak-hickory association of the Ozarks and adjacent territory may be conceived of as having arisen.

The association-segregate may arise by the advance of species and by increase in range, climate and migration capacity then exerting selective influences bringing about the separation. Thus in the northward return of deciduous forest relatively few species have gone far, and from the mixed mesophytic forest of the southern Appalachian region the beech-maple climax association of the northern part of the deciduous forest has come. The rather unimportant beech-maple association-segregate of the mixed mesophytic climax becomes northward the beech-maple or maple-beech association, the climax of its geographic and climatic unit area. This development has gone on more or less contemporaneously in Europe, and there, too, a beech-maple association is climax over a considerable area. The absence or unimportance of a mixed or undifferentiated climax in Europe (except perhaps in the Caucasus) is due to the effects of glaciation. The beech-maple association, arising as an association-segregate from the undifferentiated mixed climax, has become, areally, one of the important associations of the deciduous forest of the north temperate zone.

The undifferentiated mixed hardwood forest of the Tertiary, of which the mixed and undifferentiated mesophytic deciduous forest of today is the shrunken remnant, is the original climax from which have come, first as association-segregates, the climax associations of the deciduous forest formation.

The term, association-segregate, is an inclusive term. It includes both consociation and faciation and, if not distinguishable, lociation, but does not imply anything as to number of dominants or area occupied. It is a dynamic term implying something as to origin and relationship. In the association with but two or three dominants, segregation of the dominants usually results in the formation of consociations. Consociation, both by

definition and usage, "is characterized by a single dominant. The associa-
tion is actually a grouping, the consociation is pure dominance." (Clements,
'28, p. 130). Clements, in correspondence ('35), states that "opinions may
well differ as to the percentage necessary to constitute a consociation, but
the idea is essentially the same." In the association with a number of
dominants, segregation of the dominants seldom results in pure (or approxi-
mately pure) dominance of one of the dominants of the association; rather,
segregation results in regrouping of the dominant species into all the com-
binations possible for the number of dominants originally concerned.
Lately, faciation and lociation have been used for certain expressions of such
complex communities as exist in the southern deciduous forest area (and
in other comparable communities).

"Of the divisions of the association, the faciation is climatic, the effects
of the more recent climatic migrations being discernible in its structure,
while the lociation is in part edaphic." (Clements, '30, p. 237.) A certain
area difference is implied between the two and Clements suggests the use
of faciation for groupings "if they cover large areas within the association
or recur frequently in their proper site" (in correspondence). Shelford ('32,
p. 111) also distinguishes between the two terms on a basis of magnitude of
area covered. This entails at the outset a knowledge of area not attainable
except with extensive field work; what may at first appear to be a lociation
may later prove to be a faciation. If the formation of which such communi-
ties are a part had been studied in its entirety, as for instance has grassland,
this difficulty might not arise. But the American deciduous forest forma-
tion has never been adequately treated as is demonstrated by the prevalence
and persistence of the idea of three associations or the "threefold differen-
tiation of the formation" and the recognition of only "three related asso-
ciations, namely: (1) maple-beech, (2) oak-chestnut, and (3) oak-hickory."
(Weaver and Clements, '29, p. 453.) In actual practice, moreover, one is
confronted by the fact of equivalence as to climax status of consociation,
faciation and lociation; by the fact that all three are segregates of a more
complex community. Yet one term is applicable to one community, an
entirely unlike term to another community, even though the outstanding
difference (in any one geographic area) may be merely one of *number* of
dominants. Of course, no two dominants are exactly alike in behavior, in
competition, in reaction. Yet there may be equivalence *in rank* whether
one or more dominants are concerned. It is because no two dominants are
exactly alike (although theoretically this may be possible) that the com-
ponents of complex communities segregate in all manner of ways, producing
a great variety of communities. It is these communities which it is pro-
posed to call *association-segregates*.

It is not proposed to consider expressions of developmental units (asso-
cies) as association-segregates even though they be segregates of a relatively
complex community. For such segregations of developmental communities

the term *associes-segregate* should be used. The associes-segregate bears the same relationship to the consocies, facies and locies as does the association-segregate to the corresponding climax units. Examples of associes-segregates may help to clarify the concept.

On the Illinoian till plain of southwestern Ohio (Braun, '36) the initial forest stage in its most complex form is a pin oak-red maple-elm-sweet gum associes. This is, however, seldom represented in this condition, but more often by various segregates in which one of more of the dominants of the associes are locally dominant. Thus there are pin oak consocies and red maple consocies; also there are communities in which red maple and elm are co-dominant; others in which pin oak and sweet gum are co-dominant; still others in which red maple, elm and sweet gum together share domi-nance. These communities are all alike in that they are initial forest stages in the hydrarch succession of these plains. They differ, of course, in reactions, and these differences are reflected in later seral stages. But to apply to these co-ordinate communities different terms implies a difference of rank undesirable in a developmental or dynamic study. The use of associes-segregate for these developmental stages emphasizes similarity in rank and emphasizes the relation to or derivation from the associes. The term will be especially useful where consocies, facies and locies of the same developmental rank exist side by side.

The associes-segregate is a seral unit; the association-segregate a climax unit. It is this climax concept which is by far the more important because it helps to clarify the interpretation of the relationships of associations in a complex formation such as the deciduous forest. We may conceive of the deciduous forest climax as made up of associations and association-segregates.

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# A BOG AT HARTFORD, MICHIGAN

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In the middle of August 1927 I had the pleasure of visiting Professor Cowles in Chicago. In company with him, Professor Geo. D. Fuller and Dr. H. Kurz, I made an excursion into Michigan, where the Hartford bog, 3.5 miles east of Hartford, the Baroda bog, 1 mile east of Baroda, and the magnificent sand dunes at Sawyer were visited.

At the Hartford bog some borings were made, and from one of these a complete series of samples was collected for a pollen analysis. I would like on this occasion to give the botanical notes and the results of the borings and of the pollen analyses.

## VEGETATION

The Hartford bog occupies the margin of a basin, the center of which is a rather large lake. It is not surrounded by a wet marginal ditch, but has a surface practically level or slightly sloping towards the center (the water level). The margin of the bog is covered with a stand of rather large birch trees. The following species were noted:

| | |
|---|---|
| *Betula lutea*, dominant | *Vaccinium corymbosum* |
| *Acer rubrum* | *Aralia hispida* |
| *Liriodendron tulipifera* | *Aspidium spinulosum* |
| *Pyrus melanocarpa* | *Campanula americana* |
| *Prunus serotina* | *Osmunda cinnamomea* |
| *Sambucus racemosa* | *Maianthemum canadense.* |

Nearer the lake the birch wood is younger and more mixed with *Acer rubrum* and *Larix laricina*. The latter seems to be the first tree to invade the open bog area. In these younger parts of the wood *Sphagnum squarrosum* and *Sph. angustifolium* were found in the bottom layer. Along the border of the wood *Woodwardia virginica* formed an edging, which also contained some *Habenaria blephariglottis* and *H. ciliaris;* then the open bog area followed. The most prominent plant sociation here was the *Chamaedaphne–Sphagnum palustre*–soc., where the following species were noted:

| | |
|---|---|
| *Andromeda glaucophylla* | *Impatiens biflora* |
| *Vaccinium macrocarpon*, common | *Sagittaria* sp. |
| *Asclepias incarnata* | *Sarracenia purpurea*, common |
| *Decodon verticillatus* | *Eriophorum virginicum*, common |
| *Epilobium palustre* var. *monticola;* | *Nymphaea advena* |
|     = *E. lineare* | *Sphagnum* sp. |
| *Hypericum virginicum* | |

The *Chamaedaphne* sociation was followed by a narrow strip of *Eleocharis rostellata–Sphagnum palustre*–soc. with the following species among others:

| | |
|---|---|
| *Spiraea tomentosa* | *Hypericum virginicum* |
| *Ilex verticillata* | *Dulichium arundinaceum* |
| *Epilobium molle* | *Typha latifolia.* |

Many of these species really belong to the high thicket-like border towards the open water. The pioneer of the quaking mat, invading the lake, was *Decodon verticillatus*, which by means of its peculiar curved stems, equipped with floaters, appeared to walk on the water surface among *Nymphaea* and other water plants.

In the thicket behind the *Decodon* the following plants were observed:

| | |
|---|---|
| *Salix* sp. | *Scutellaria lateriflora* |
| *Rhus vernix* | *Typha latifolia* |
| *Spiraea tomentosa* | *Viola pallens* |
| *Osmunda regalis* | *Rynchospora alba* |
| *Aspidium thelypteris* | *Sagittaria latifolia.* |
| *Eupatorium perfoliatum* | |

The zones here described were mostly rather compressed. This was true especially of the open *Sphagnum* societies between the migrating wood and the thicket border, but at the place where the first boring was made, however, the open area was somewhat broader as will be seen from the sketch showing the distribution of vegetation (fig. 1).



oo *Betula lutea*      ## *Acer rubrum*

ww *Woodwardia -edge*      xx *Larix*
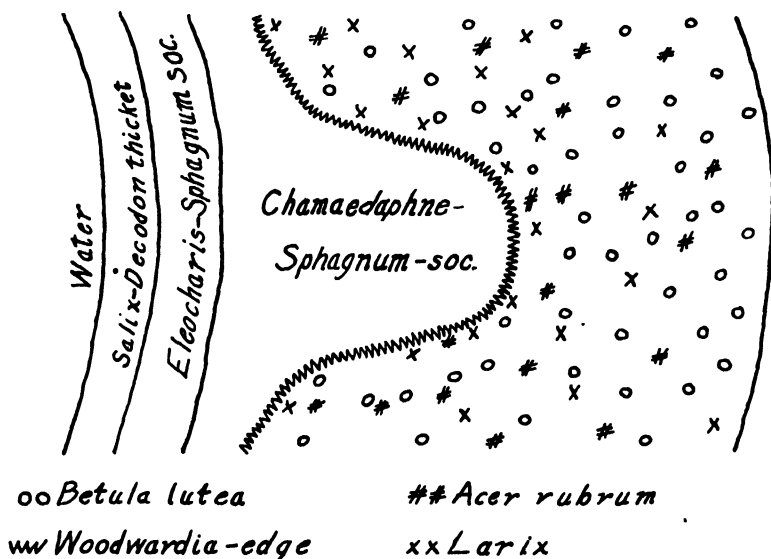
FIG. 1. Sketch of the vegetation at the Hartford bog at the place where the borings were made.

## STRATIGRAPHY

The borings were made with the ordinary Swedish peat borer (Hiller's peat auger), 9 m. in length and with 50 cm. sampler. The degree of decomposition (humification) of the peat is given in symbols, $H = 1$ to $H = 10$ according to the von Post scale, where $H = 1$ means practically undecomposed peat, $H = 10$ completely decomposed peat.

The first profile was made on the open *Chamaedaphne* area, and here an almost complete series of samples was collected. The second profile was bored in the birch wood about half way between the first profile and the margin of the bog; because of lack of time samples were taken only from every meter. At the third boring, half way between the second one and the margin, samples were collected only from the surface layers and from the bottom. Finally, a fourth boring was made near the margin (fig. 2).

### Boring 1.   Chamaedaphne–Sphagnum bog

*a.*    50 cm.    *Sphagnum palustre* peat, $H = 1$.

*b.*    15 cm.    *Carex–Sphagnum palustre* peat, $H = 1$.

*c.*   115 cm.    *Carex* peat, $H = 8$, with some *Sph. palustre* and seeds of *Nymphaea* and *Potamogeton*.

*d.*    70 cm.    *Carex* peat, $H = 3–5$, with some *Drepanocladus*.

*e.*   200 cm.    Water with debris of *Carex* peat.

*f.*    90 cm.    Lake mud (gyttja) with rhizoms and roots of *Carex* and in the lower 25 cm. with *Drepanocladus*.

*g.*     5 cm.    *Drepanocladus* peat.

*h.*    35 cm.    Lake mud with *Carex* and *Drepanocladus*.

*i.*     5 cm.    *Drepanocladus* peat.

*j.*    12 cm.    Lake mud with *Carex* and *Drepanocladus*.

*k.*    53 cm.    Sandy and silty lake mud, in the upper part brownish, in the lower one bluish grey; in the middle with many rhizomes of some water plant.

*l.*    80 cm.    Lake mud with *Drepanocladus* in the upper part, some *Carex* and *Sphagnum* in the lower one, and rhizomes of some water plant at different horizons.

*m.*     2 cm.    Light grey sand.

*n.*     8 cm.    Sandy and clayey brown lake mud.

*o.*    20 cm.    Bluish grey, silty clay, with a piece of wood.

At 7.60 m.   The auger in sand.

### Boring 2.   Betula lutea forest

Concerning the second profile I have to confine myself to the character of the layers from which samples were collected:

0.0–1.0 m.:   15 cm. wood peat, $H = 9$.

                   15 cm. *Carex–Sphagnum* peat, $H = 2$.

                   70 cm. *Carex* peat, $H = 5$.
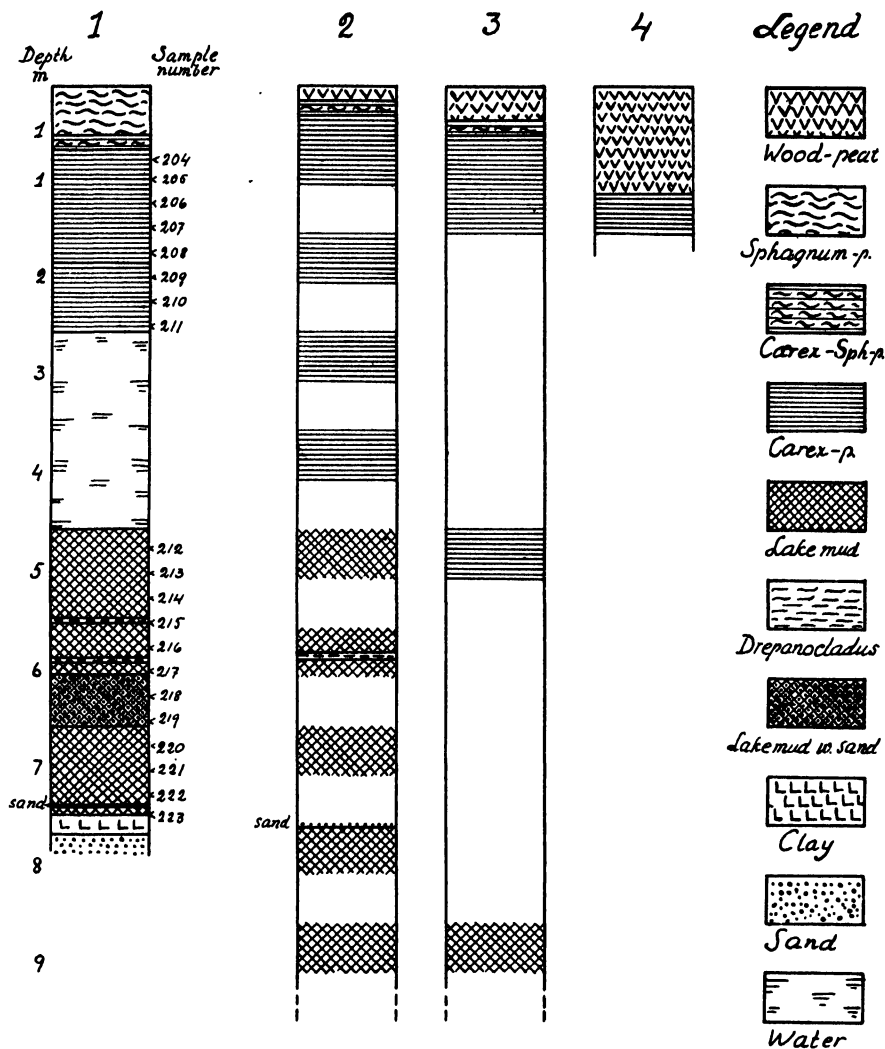
FIG. 2.  The four profiles through the Hartford bog.

1.5–2.0 m.: *Carex* peat, $H = 5$.

2.5–3.0 m.: *Carex* peat, $H = 7$.

3.5–4.0 m.: *Carex* peat, $H = 7$.

4.5–5.0 m.: Lake mud with some *Carex*.

5.5–6.0 m.: 25 cm. lake mud with *Carex*.

       7 cm. *Drepanocladus* peat.

      18 cm. lake mud with *Drepanocladus* and *Carex*.·

6.5–7.0 m.: Lake mud.

7.5–8.0 m.:  2 cm. sand.

      48 cm. lake mud.

8.5–9.0 m.:   Lake mud.

No bottom struck.

### Boring 3. Betula lutea forest

0.0–0.5 m.:   35 cm. wood peat, $H = 9$.

               15 cm. *Carex–Sphagnum* peat with much shrub debris.

1.0–1.5 m.:   *Carex* peat, $H = 4$, with much *Vaccinium oxycoccus*.

4.5–5.0 m.:   *Carex* peat.

8.5–9.0 m.:   Lake mud.

No bottom struck.

### Boring 4. Betula lutea forest

110 cm.   Wood peat, $H = 9$.

 40 cm.   *Carex* peat, $H = 5$, with some *Sphagnum*.

Since the distances were not measured and the surface of the bog not levelled, the different profiles cannot be exactly connected. Nevertheless, I have tried to draw a profile sketch in order to illustrate more clearly the stratification (fig. 3).

The development in this part of the basin may be summarized as follows. During the first stages (after the recession of the ice) clay and clayey lake mud were sedimented in the open lake. These sediments were followed by
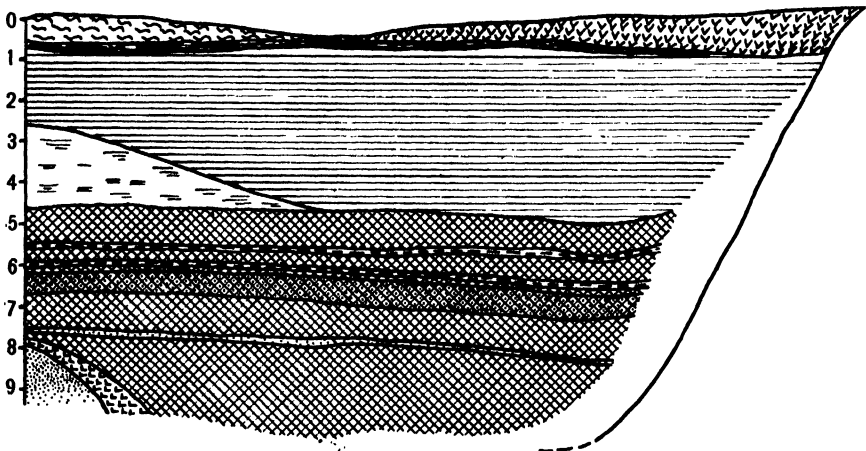


Fig. 3. Sketch of the stratification of the Hartford bog. For legend see figure 2. Depth in meters.

ordinary lake mud, which seems to have formed a rather thick layer in the deepest part, but only a thin one at the place where the first boring was made. Over this lake mud a thin layer of sand was deposited, and then the sedimentation of lake mud continued, until a layer of 80 cm. in thickness (now) was formed. During the next stage the lake mud was mixed with sand and

clay—eventually a result of increasing water flowing to the lake (increased rainfall?, lower temperature?) ; this layer is about 50 cm. thick. Then again ordinary lake mud was formed. During this period *Drepanocladus* seems to have been very common on the bottom of the lake, and at two different, rather short periods, this moss has completely covered the bottom and formed the pure *Drepanocladus* peat.

The open lake was then overgrown by a quaking *Carex* mat, which near the shore has sunk down to the lake mud surface, while there is still a layer of water between the lake mud and the quaking mat in the outer part.

In rather recent times *Sphagnum* invaded the *Carex* swamp, and somewhat later the *Chamaedaphne–Sphagnum* bog developed. Contemporaneously or perhaps earlier, as soon as the *Carex* peat surface near the margin was dry and firm enough, the birch forest migrated into the swamp.

### Pollen Analyses

The pollen analyses of the series of samples from boring 1 were made at the Växtbiologiska institutionen (Plant Biological Institution) of the University at Uppsala by Mr. Carl Larsson, to whom I want to express my sincere thanks for valuable assistance.[1] The result is given in table 1 and for some species and groups of species also in figure 4.

It is easy in the tables and diagrams to distinguish three very obvious periods or stages, viz.

*1. The coniferous forest stage.* During this stage the coniferous trees probably formed the main part of the forest, their contribution to the pollen flora being 83.6 per cent. *Picea* and *Abies* are the most prominent genera; both of them disappear in the later periods.

*2. The deciduous forest stage.* This stage is characterized by low percentages for the coniferous trees, among which *Pinus* is the most important. At the beginning as well as at the end of the period the percentage, however, is greater than during the whole intervening time. Among the deciduous trees the *Quercus* species dominate.

*3. Mixed forest stage.* The coniferous trees (*Pinus*) contribute with about 30 per cent of the pollen, and among the deciduous trees oak is still dominating. *Carpinus* and *Juglans* disappear in the beginning of the stage.

There is, as expected, full coincidence with the periods, which have already been pointed out by Fuller, Houdek, Sears, Voss, and others.[2] The development of vegetation thus seems to suggest changes in the climate, corresponding to those which have already been demonstrated for Europe.

It should be noted that the first stage is represented only by a single sample. If the collecting of samples had taken place in profile 2 instead of in

[1] Concerning the technique of pollen analysis I refer to recent contributions of Erdtman, Sears, Voss and others.

[2] See bibliographies on pages 487, 498 of this issue.

Table 1. Percentages of fossil pollen in the Hartford bog

| Depth m. | Sample number | Number of pollen grains counted | Abies | Picea | Pinus | Tsuga | Acer | Alnus | Betula | Carpinus | Carya | Corylus | Fagus | Fraxinus | Juglans | Liquidam-bar | Ostrya | Quercus | Tilia | Ulmus |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0.70 | 204 | 162 | — | — | 35.1 | — | 2.5 | 0.6 | 4.9 | — | 6.2 | 2.5 | 16.7 | — | — | — | 1.9 | 25.8 | 1.9 | 1.9 |
| 0.95 | 205 | 151 | — | 0.7 | 30.0 | 2.0 | — | 1.3 | 1.3 | — | 2.0 | 0.7 | 15.3 | 0.7 | — | — | — | 40.0 | 0.7 | 5.3 |
| 1.20 | 206 | 162 | — | — | 30.2 | 0.6 | 1.2 | 0.6 | 3.7 | — | 4.3 | 1.9 | 19.1 | 1.2 | — | — | — | 34.1 | 0.6 | 2.5 |
| 1.45 | 207 | 153 | — | 0.7 | 28.0 | 1.3 | 1.3 | 1.3 | 3.3 | — | 0.7 | — | 19.0 | — | 0.7 | — | — | 39.1 | 2.0 | 2.6 |
| 1.70 | 208 | 158 | — | — | 15.2 | 1.3 | 2.5 | 1.9 | 3.2 | 1.3 | 6.3 | 0.6 | 27.1 | 1.9 | 1.3 | 0.6 | 0.6 | 31.8 | — | 4.4 |
| f·95 | 209 | 153 | — | — | 5.9 | 2.6 | 3.3 | — | 6.5 | — | 6.5 | 0.7 | 26.2 | 3.3 | 4.6 | — | 3.9 | 30.0 | 2.6 | 3.9 |
| 2.20 | 210 | 156 | — | — | 5.1 | 1.3 | 0.6 | — | 1.9 | 0.6 | 5.8 | — | 30.1 | 3.2 | 3.2 | — | — | 32.8 | 2.6 | 12.8 |
| 2.45 | 211 | 157 | — | — | 4.5 | 1.3 | 1.9 | 0.6 | 3.2 | 0.6 | 7.6 | — | 28.0 | 1.9 | 1.3 | — | — | 40.2 | 1.3 | 7.6 |
| 4.70 | 212 | 152 | 0.7 | — | 5.3 | — | 0.7 | 0.7 | 1.3 | 0.7 | 3.3 | — | 16.4 | 2.0 | 2.0 | — | 1.3 | 53.1 | 0.7 | 11.8 |
| 4.95 | 213 | 152 | — | — | 2.0 | — | 3.3 | 2.6 | 2.6 | 0.7 | 2.6 | 0.7 | 17.8 | 3.3 | 1.3 | — | — | 50.4 | 2.6 | 9.9 |
| 5.20 | 214 | 152 | — | — | 9.2 | 2.6 | 1.3 | 0.7 | 1.3 | 0.7 | 4.6 | — | 20.4 | 2.6 | 0.7 | — | — | 47.4 | 0.7 | 8.0 |
| 5.45 | 215 | 152 | — | — | 9.2 | 2.0 | 1.3 | 0.7 | 1.3 | 0.7 | 4.6 | — | 11.2 | 1.3 | 0.7 | — | — | 55.2 | — | 11.8 |
| 5.70 | 216 | 162 | — | — | 6.8 | — | 3.8 | 0.6 | — | 2.5 | 1.9 | — | 13.6 | 4.3 | 2.5 | — | 1.2 | 46.1 | 1.9 | 14.8 |
| 5.95 | 217 | 181 | — | — | 5.5 | 0.6 | 2.2 | — | 1.1 | 0.6 | 4.4 | 1.1 | 13.8 | 7.7 | 1.7 | — | 0.6 | 49.6 | 1.7 | 9.4 |
| 6.20 | 218 | 151 | — | — | 8.6 | — | 7.3 | — | — | 0.7 | 10.6 | 0.7 | 9.3 | 2.0 | 1.3 | — | 1.3 | 44.3 | — | 13.9 |
| 6.45 | 219 | 167 | — | — | 12.0 | — | 1.8 | — | 0.6 | — | 3.6 | · | 13.2 | 0.6 | 1.2 | — | — | 56.2 | 1.8 | 9.0 |
| 6.70 | 220 | 152 | — | — | 4.0 | — | 2.0 | — | 0.7 | — | 7.9 | — | 7.2 | 0.7 | — | — | 0.7 | 53.8 | 0.7 | 22.3 |
| 6.95 | 221 | 154 | — | 0.6 | 14.9 | — | 2.6 | — | — | — | 2.6 | — | 1.9 | 1.3 | — | — | — | 59.3 | 0.6 | 16.2 |
| 7.20 | 222 | 158 | — | — | 23.4 | — | 1.3 | 0.6 | 1.9 | — | 3.2 | 1.3 | 0.6 | — | 1.3 | — | 1.3 | 49.4 | 2.5 | 13.9 |
| 7.45 | 223 | 104 | 30.8 | 36.5 | 16.3 | — | — | 1.9 | 1.0 | — | 1.0 | — | — | — | — | — | — | 9.6 | — | 2.9 |

Fig. 4. Pollen diagram from profile 1 of the Hartford bog. In order to avoid confusion the curves for *Fagus*, *Ulmus* and *Acer* a. o. are drawn separately. "*Acer* a. o." comprises *Acer*, *Carpinus*, *Carya*, *Fraxinus* and *Juglans*.

profile 1, it is very likely that this first stage would have been much more richly represented. Although I am not inclined to draw conclusions on the basis of a single profile, I would like to point out that the transition from the first to the second stage seems to be synchronized with the sand layer in the lake mud. On the contrary, there does not seem to be any obvious strati-graphical limit contemporaneously with the transition between the stages 2 and 3.

During the third stage a rather striking change seems to have taken place in relatively recent times, being represented by the sample at the top of the series. This change is reflected in the increasing percentages for *Pinus*, *Betula*, *Carya* and *Corylus*, and in the decreasing figures for *Quercus* and *Ulmus*. This change seems to coincide with the transition from the *Carex* swamp to the bog societies rich in *Sphagnum*.

There seems to be some evidence to show that the large second stage might be subdivided. The first subdivision, 2a, is characterized by very high figures for *Quercus* and *Ulmus*, the latter reaching its maximum during

this period, further by a strongly increasing frequency of *Fagus* and relatively low figures for a number of other deciduous trees, such as *Fraxinus* and *Acer*. During the second substage, *2b*, *Quercus* declines, *Ulmus* plays as important a role as earlier, *Fagus* keeps its position, *Carpinus* appears for the first time in the profile, and a number of deciduous trees, such as *Juglans*, *Fraxinus* and *Acer*, get higher frequencies than earlier. During the stage *2c* the oak and beech increase, while *Fraxinus*, *Acer* and *Carpinus* decline. Finally, during the stage *2d*, the oak decreases and the beech increases very much, while a number of other deciduous trees, *Carya*, *Juglans*, *Ostrya* and *Carpinus*, reach their maxima; the same is true also for *Tsuga*.

The changes to which I have called attention may be of local interest only, and the variations in the figures do not necessarily suggest regional changes in the vegetation. It should, however, be pointed out that the transition from *2a* to *2b* very closely coincides with the limit between the lake mud and the clayey lake mud at the depth of 6.5 m. and the transition from *2c* to *2d* with the limit between lake mud and *Carex* peat.

## SUMMARY

The vegetation of the Hartford bog shows a very obvious zonation from birch wood (*Betula lutea*) at the margin of the bog through open bog sociations to the border thicket at the water surface.

The bog has been formed by filling up the marginal zones of the original lake and has been built up by different kinds of lake mud, *Carex* peat, wood peat and *Sphagnum* peat.

The pollen analyses reveal three rather obvious stages in the development of the forests of the region, the coniferous, the deciduous and the mixed forest stage. Moreover, the pollen flora suggests the possibility of a more detailed subdivision of the deciduous forest stage.

Most of the deciduous trees were present at the beginning of the deciduous forest stage; *Carpinus*, however, does not seem to have migrated, until the beginning of the stage *2b*. The same seems to have been the case with *Tsuga*.

Some of the transitions between the different stages coincide with stratigraphical limits.

## ACKNOWLEDGMENTS

# NOTES AND COMMENT

## A Stick for Measurement of Reproduction

While making reproduction studies in permanent sample plots, the writer recognized the need for a measuring-stick which could be read easily in heavy reproduction.

*Description of the stick:* All measurements are in feet and tenths, which is much simpler than feet and inches. A planed stick of light pine 4.5' long, 1.5" wide and .75" in thickness was used. It was marked off at the following points: .1', .5', 1', 2', 3', 4', and 4.5'—the space between each point being painted in a contrasting color. The accompanying diagram illustrates the marking and coloring of the stick.
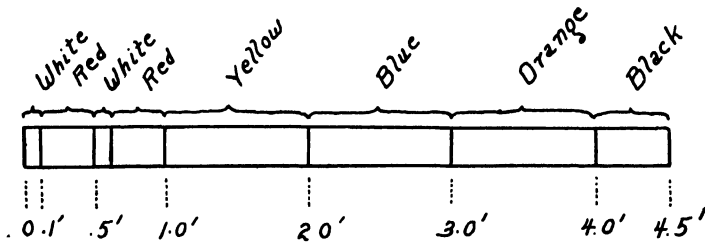


FIG. 1.

The use of such a stick permits more rapid measurements than are possible with other methods. Confusion between various height-classes, often experienced when using a notched stick, is eliminated. Moreover, the vivid colors can be distinguished through heavy covers of reproduction.

The stick is widely adaptable to any work; for example, the lower classes, viz., .1' and .5', may be omitted if the stick is intended for use in a region where the work does not require such fine measurements.

A similar stick of any desired length could be made, the additional length being painted in the same series of color. The marking may be varied to meet the specific needs of the purpose intended.

The stick is recommended for measuring different height classes of tree reproduction, small shrubs and plants; also for getting breast height or for marking the diameter breast high (d.b.h.) point.

-William E. Brown

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## An Improved Pantograph for Mapping Vegetation

Since its introduction by Hill[1] in 1920, the pantograph has been widely used by the Forest Service and other agencies as a means of rapidly and accurately mapping the vegetation of meter quadrats. The Intermountain Forest and Range Experiment Station has

[1] **Hill, Robert R.** 1920. Charting quadrats with a pantograph. *Ecology* 1: 270–273.

improved the instrument in recent years to provide greatly increased accuracy, speed, and ease of operation.

A light but rigid arm of tubular aluminum which provides a maximum degree of accuracy has been adopted. Large offset bearings eliminate torque, so objectionable in the original arm, and permit compact folding. The length of the removable pointer is easily adjusted to the contour of the plot. Incorporated in the arm is a new pencil supported slightly above the paper by a light spring. When a plant is to be mapped, the pencil is lowered into the writing position by a light pressure of the finger. To facilitate sharpening, the entire pencil can be easily slipped out of its socket.
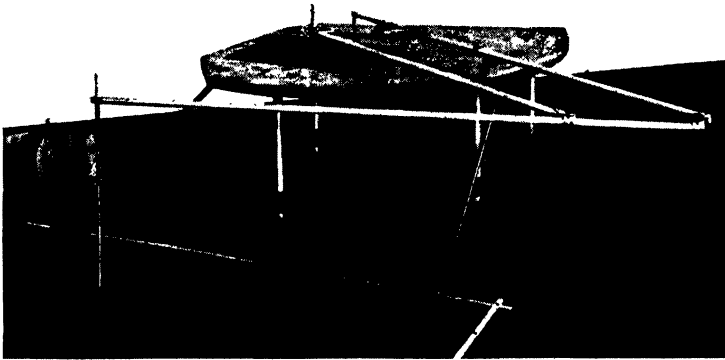


FIG. 1.   The improved pantograph as set up for field use.

The plywood table is fitted with rigid steel legs which are adjustable so that on uneven terrain the top may be made to parallel the surface of the quadrat without the use of blocks, rocks, or other material. Two steel "tie in" legs serve to orientate the board with respect to the plot. A hard smooth writing surface is provided by a bakelite or pressed wood inlay. Four easily replaceable corks are set in the corner of the inlay to receive the thumb tacks that hold the map sheet in position. If corks and thumb tacks are not desired, "scotch tape" serves very well to keep the paper in place. To insure a smooth hard track for the roller on the arm, the edge of the board is inlaid with an arc of maple, bakelite or metal.

Complete specifications and instructions for the construction of the arm and table are on file at the Intermountain Forest and Range Experiment Station and are obtainable on request.

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CONTRIBUTIONS TO TEXAN HERPETOLOGY. II. SOME OBSERVATIONS AND AN EXPERIMENT ON THE WORM SNAKE, LEPTOTYPHLOPS

The burrowing worm snake of Texas is *Leptotyphlops dulcis* (Baird and Girard). It is a characteristic inhabitant of moderately sandy, semi-arid prairies of the lower

middle west, where it may be found either in the vicinity of trees or away from them. The present Texan series was secured between March 29 and April 24, 1931, from under flat rocks on hillsides where they were very frequently associated with the banded and unicolor phases of the prairie snake *Sonora semiannulata,* and with the collared lizard *Crotaphytus collaris.*

On the morning of March 30, two living examples of *Leptotyphlops* from Palo Pinto County were brought into the laboratory and introduced into a cage having dry sand at one end and wet sand at the other. Within two hours both individuals had burrowed into the dry sand. By 6:00 P.M. it was noticed that the wet sand had lost enough water by evaporation to become only "moist sand" and that the two snakes had migrated from the dry to the damper area. During the next three days repeated examinations continued to show both snakes in the moist sand, with but a single exception. This experimental evidence tends to indicate that *Leptotyphlops dulcis* requires a moist, but not wet, medium in which to live and that it naturally selects this environment when given free choice in the matter. Individuals are not common under rocks during the summer. This suggests that the snakes burrow downward as the surface layer dries.

Because of the relative rarity of *Leptotyphlops dulcis,* the following county reports are of interest:

CAMERON: Brownsville (R. D. Camp). COLEMAN: Santa Anna (April 24, 1931). COMANCHE: 4 mi. W. Comanche (April 24, 1931). DENTON: Denton (B. B. Harris, April 1933). ERATH: 3 mi. S.W. Dublin (April 24, 1931). McCULLOCH: Brady (Gus Wagner). McLENNAN: Waco (Hurter Coll., 1910). MONTAGUE: 4 mi. N.W. Bowie (April 17, 1931). PALO PINTO: 3 mi. W. Millsap (March 29, 1931). STARR: Riogrande (U. S. N. M.).

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### RANGE CAPACITY DETERMINATION

The commercial value of a range is primarily determined by the number of livestock it is capable of supporting. A method of measuring this capacity is, therefore, highly desirable as a key to value. By knowing its capacity, it is also possible to avoid overgrazing a range rather than to find out too late that it has been ruined by erosion and undesirable plant succession. To ruin a range is easy; to improve it, difficult.

The methods now used for determining the capacity of western ranges are based chiefly upon estimation. The oldest, and still the most used, is an ocular survey based on past experience and comparison. This method is obviously subject to great error. The more scientific methods are usually based upon an estimate of the percentage of each plant of each species which is consumed by stock, and the percentage of the area in the pasture which is covered by each species. The inaccuracy of such a determination is made evident by the fact that it is obtained through the use of two estimated figures, neither of which gives an exact picture of the range resources in question.

A method has been devised by which it is believed the capacity of a range can be determined with both greater ease and greater accuracy than by methods commonly used. For demonstration, a mixed-grass prairie near the foothills west of Fort Collins, Colorado, was selected. This area is essentially a western wheatgrass, *Agropyron smithii* Rydb., range with an open mat of grama grass, *Bouteloua gracilis* (H. B. K.) Lag., and buffalo grass, *Bulbilis dactyloides* (Nutt.) Raf.

In 1931, the area selected was used for late spring and summer range. The rainfall in the spring was sufficient to give good early growth, but the unusually dry hot summer caused most plants to stop growth relatively early. Many were dry and brown by fall, when these studies were made.

Western wheatgrass, since it makes up the bulk of the forage, was selected as a basis upon which to make capacity calculations. Since this species is the most important, it should not be overgrazed. Therefore, when wheatgrass is grazed to capacity this range should be considered fully utilized. Obviously a certain percentage of the stalks should be left for reproduction and possibly early feed for the following year. Various workers have placed this percentage at 15 to 25. An average figure of 20 per cent seems to be approximately correct and was used as the basis for computations. The range was, then, considered utilized when 80 per cent of the stalks of wheatgrass had been nipped off by stock. Having made these conclusions, no attention needed to be given to how much any other plant was grazed nor to what percentage of the area it occupied. Nothing concerned the investigator except the percentage of the wheatgrass stalks which had been grazed.

To find this percentage of utilization, a count of the grazed and ungrazed stalks was necessary. Therefore, twelve quadrats, each one meter square, were placed in a 145 acre pasture which had been grazed to about its capacity by mixed grade cows. To eliminate any error from personal selection, these quadrats were located at definite distance intervals within the pasture so that all the area was represented. The quadrats were carefully gone over and the actual number of stalks of wheatgrass on each was determined. A record was also made of the number of stalks which had been grazed (fig. 1).



Fig. 1. The grazed and ungrazed stalks of western wheatgrass can easily be distinguished.

Averages of the twelve quadrats gave the following figures:

Average number of stalks per square meter ...................... 119
Average number of stalks grazed ............................... 88
Average number of stalks ungrazed ........................... 31

From these figures it was calculated that 74 per cent of the stalks had been grazed. Since 74 is 92.5 per cent of the 80 per cent which should be grazed, the utilization was 92.5 per cent at the time the count was made.

The capacity of the range could then be computed from the records of stocking. There were 15 head of stock on the 145 acres for 5.5 months. The number of cows multiplied by the number of months gives 82.5 cow-months grazed at the time the count was made. Since the utilization at that time was only 92.5 per cent of the desired amount, the 100 per cent capacity, or cow-months possible without injuring the range, would be 89.2. If the owner runs 15 cows he should, therefore, keep them on this pasture for approximately six months.

If the possible cow-months (89.2) is divided by the number of acres (145) a figure 0.615 is obtained which is the number of months one acre will support one cow. The figure so obtained should apply fairly well to all mixed-grass prairie range of the western wheatgrass type. The ease of making the determination, however, makes frequent checking practical and it is highly desirable.

Such an analysis should give an accurate figure for the year the test is made, but in years of lesser rainfall it might prove necessary to repeat the count in order to avoid injuring the range.

If, over a period of time, it is found that the range is not being maintained or improved it would indicate that 20 per cent of the stalks is not sufficient for propagation, and the amount left ungrazed should be increased.

## SUMMARY

A method is advanced by which it is possible to measure accurately the stock carrying capacity of western wheatgrass range in the mixed-grass prairie. It is based upon a simple count of the grazed and ungrazed stalks of wheatgrass within regularly located quadrats.

A measurement by this method indicated that this range will carry one cow on one acre for 0.615 months. This figure is believed to be applicable to western wheatgrass range rather generally through the semi-arid mixed-grass prairie grazing land.

This method is sufficiently accurate, rapid, and simple to make its use practical and it is believed to be an improvement over usual methods.

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# ECOLOGY

## SOME WINTER RELATIONS OF THE WHITE-TAILED DEER TO THE FORESTS IN NORTH CENTRAL MASSACHUSETTS

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Although the white-tailed deer, *Odocoileus virginianus virginianus*, has been used by the white man as an important source of food and leather since the first New England settlements and is the only large game animal to maintain itself following the settlement of the region, little exact knowledge of its habits and requirements has been recorded. Considerable popular literature is to be found on the species, but little is of a specific nature. Within the past few years a beginning of studies has been made in Pennsylvania (Clepper, '31; Forbes and Overholts, '31; Forbes and Bechdel, '31; Frontz, '30) and in the Adirondacks (Townsend, Smith and Spiker, '33). The habits of the animal vary so widely in different regions that local studies are necessary to make an intelligent approach to its management. With this in mind the present study was undertaken as a start toward determining some of the factors necessary for the best local development of the species and of the means by which forestry can contribute to the attainment of this development.

Specifically the objects were to find for north central Massachusetts (1) what food was eaten by the white-tailed deer during winter, (2) how its feeding habits were correlated with ecological succession, (3) whether preferences were shown for various forest types for food or shelter, (4) the general characteristics and habits of the animal. The study had two main divisions: field observations and stomach analysis. The general field practice was to follow the deer tracks on snow, examining and tallying all feeding along the route. All forest types passed through were noted, as were cases of bedding, loafing, etc. The stomachs were secured principally during the hunting season in early December, with some over the period from November to April. These were tagged as collected, a standard mimeographed form was filled out recording pertinent data for each, and they were placed in a formalin solution until

examined. A total of 24 stomachs was analyzed. Stomachs were mainly secured by cooperation with state game officials and with local residents of Petersham.

With one exception field observations were confined to the town of Petersham. This exception was an examination of Rattlesnake Mountain in the town of Erving, which was the winter rendezvous of a large number of deer.

## DESCRIPTION OF REGION

The town of Petersham, covering some 24,000 acres, is situated in northern Worcester County, Massachusetts, and is quite typical of much of the surrounding region. It is part of what foresters call the "transition zone." This term describes the overlapping of the northern forest as represented by such species as beech, *Fagus grandifolia*, yellow birch, *Betula lutea*, and hard maple, *Acer saccharum*, and the central forest in which oak predominates. Species representing both forest regions are to be found in Petersham. For the purpose of this study the areas were divided into nine types which do not strictly conform to the standard as set up by the Society of American Foresters (Hawley, R. C. et al, '32) for this region. A rigid adoption of that standard was impractical because some of the more important ones were not strictly forest types.

The forest history of Petersham will give some conception of the present composition and condition of the forest. The original forest was composed largely of hemlock, *Tsuga canadensis*, and hardwood with an interspersion of white pine, *Pinus strobus*. This original forest was cut and much of the land cleared for farming between the years 1700 and 1830. Farming extended rapidly in this period. With the impetus given western settlement by the development of the railroads, however, farming in the Petersham region became increasingly less profitable, and land abandonment set in. At the peak of farming around 70 per cent of the land area of the town was cleared, but at the present time only about 25 per cent is in village and agricultural use. As the fields and pastures were left to nature, white pine seeded in and reclaimed the areas thus abandoned. As the pine matured, important industries grew up, using the lumber produced. Its principal uses were in box manufacture, match stock, and sash and blind construction. Fortunes were made in the heyday of harvesting the pine woodlots. Today most of this type has been logged off.

Pine did not follow pine on the better soils of this region, and after pine cuttings the next great forest succession was hardwood, of which the first crop was often of valuable species. The more valuable ones were present under the pine as advance growth. This first hardwood crop was cut largely for cordwood, although many stands are still left and are of sawlog size. When the good hardwood was removed, the stand sprouted with characteristic persistence. All would have been well silviculturally except that the second crop of hardwood did not have as good composition as the first, and forest

weeds were present to a much greater degree than before. Sprouts from the larger stumps were coarse and often defective. The most serious of the weeds were gray birch, *Betula populifolia*, fire cherry, *Prunus pennsylvanica*, and red maple, *Acer rubrum*. These are fast growing and got their first real foothold in some of the original pine cuttings where hardwood advance growth was lacking. When the first hardwood crop was removed, the weeds increased their percentage composition of the stand; and in the usual present hardwood stand, two cuttings removed from the old field pine type, they form a large and ever increasing proportion. Were the forest allowed to grow unmolested, the short-lived weeds would eventually drop out. In the main, we find the forests at present dominated by poor quality hardwood with a sprinkling of pine and hardwood with prospective sawtimber value.

The forest has not always followed the same trend since Colonial days. Some isolated blocks were not cut at all, some were lightly culled, and some heavily cut. Much of the area of Petersham was long maintained in field or pasture, and some of this still remains in the stage known as the old field pine type. Since, at the present time, it requires at least ten and often thirty years for an old field to revert to pine, much of the area is now in old fields covered with brush and small clumps of trees.

The topography of Petersham is much broken. The main ridges run north and south with a wide valley between them. These ridges are dissected by many local variations and cross drainages. The main drainage is to the south. In the southeast part of the town a series of minor ridges run parallel in a general northwest-southeast direction. The elevations run from 700 to 1,400 feet with the main ridges over 1000 feet.

The soils found in this region are divided into but two classes for the purpose of this work. A sandy loam, which occupies the ridges, is predominant. The other soil, which forms a distinct minority, is a sand outwash type found in the valley bottoms in the western part of the town. It is realized that this soil division is a broad one, but the purpose of including soils is to give a picture of the future for broad forest types. Soil depth is extremely variable. The entire region is underlain with granitic rock and has been heavily glaciated.

The winter during which the study was made, 1933–34, was one of the most severe in the memory of the oldest inhabitants. Temperatures down to twenty-eight degrees below zero were recorded at the Harvard Forest Headquarters and as low as — 35 degrees at lower elevations about the town. Snowfall was well over the November–March average for the past ten years. During the period of this study the snowfall was 87.75 inches, while the average for the past ten years was 52.25 inches. Not only was the snow deeper than usual, but it remained on the ground for a longer time. The ground was snow-covered from early in December until late in March.

## DESCRIPTION OF TYPES AND THEIR USE BY DEER

As has been stated, the cover types used in this study are broadly defined and are nine in number. In order of relative area in the town, they are: pure pine, young hardwood, old hardwood, pine-hardwood, old field, hemlock-hardwood, pine-hemlock, Scotch pine plantation, and old orchard.

Pure white pine is found either as a remnant of the stands which developed on old fields with heavier soils or, as occasionally happens, as a permanent pine type on the more dry and sandy soils. Due to increasing side light beneath the crowns and to a breaking up of the canopy, a heavy understory of hardwood usually develops in these stands at about fifty years of age, providing abundant deer food. No feeding by deer was observed in pine stands under thirty years old.

The hardwood types together form the greatest part of Petersham's forest cover, but the young stands vary widely from the older ones in point of deer food. These stands below the age of approximately fifteen years furnish abundant browse for the deer. Many of the intolerant species such as sumac and pasture juniper which are present up to this point are later overtopped and disappear. As the stands close in and the lower branches die, deer are unable to reach food in them. These stands are often too densely stocked to allow any except the most tolerant species to grow beneath them until the main crop trees are quite old. Then, as the crowns of some trees wear down, light is admitted enough to bring in advance growth, and deer can again reach browse.

Pine-hardwood usually occurs where stands were cut during unusually favorable years for pine reproduction, or where a pure pine stand has been cut leaving the worthless trees to grow along with the sprout hardwoods. Due to their mixed composition, these stands are often irregular in height and, as a result, produce a good variety of deer foods.

The old field type occurs as land which has been completely abandoned but which has not yet reached the forest stage. Herbaceous growth covers a large part of the type, while shrubs, light-seeded hardwoods, and volunteer pine are usually present. During the fall and early winter the old fields furnish a large part of the deer's food. Apple trees are often abundant, and these are apt to be accompanied by a rank growth of wintergreen, *Gaultheria procumbens,* dwarf raspberry, *Rubus hispidus,* pasture juniper, *Juniperus communis,* and sumac, *Rhus* spp., producing food enough in a small area to support a herd of several animals.

Hemlock-hardwood is found scattered over the town, usually on the more moist sites. The hemlock may or may not form the dominant stand. The type normally occurs on areas which were never clear cut. Due to the varying elements, this type shows more unevenness in canopy than is the case with pure stands of pine or hardwood and so it has a good variety of deer foods. This is one of the two types in which ground hemlock, *Taxus canadensis,* is found in quantity.

The pine-hemlock type occurs commonly on steep rock ledges where moisture conditions are favorable and where the remnant pine was left either by accident or because of inaccessibility. Ground hemlock is found in this type and, in point of the number of important deer foods found in it, this is one of the best.

The Scotch pine plantation type around fifteen years of age was a haunt of the deer during the severe winter, although it might be said in this connection that the species is probably not so important as the topographic location of the plantation and the cover afforded. It could probably just as well have been white pine of the same age. Although this type furnished food for the deer over a period of a week at a time, feeding was confined almost entirely to the openings and borders where hardwood trees and shrubs were present.

The old orchard type is used to describe those areas where the orchards are no longer cultivated or otherwise cared for. This is quite common on abandoned farms throughout the region. From the early trees the apple seed was spread to the surrounding country, and today escape trees are found scattered through practically every forest type. Taken together these trees furnish an abundant supply of food which was found to be very important in both fall and winter.

In any of these forest types, openings have a flora which is similar to that of the old field type.

Table I shows the foods taken by the deer or present in these types and

TABLE I.  *Cover types of the town of Petersham and the important deer foods found in them*

| Type | % town area | Eleven Most Important Species of Deer Food | | | | | | | | | | | Totals |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | a | b | c | d | e | f | g | h | i | j | k | |
| Pure pine | 30 | X | X | | X | X | X | X | | X | X | X | 9 |
| Young hardwood | 25 | X | X | | X | X | X | | 0 | X | X | 0 | 9 |
| Old hardwood | 18 | X | X | | X | X | 0 | 0 | X | | 0 | | 8 |
| Pine-hardwood | 10 | 0 | X | | 0 | 0 | 0 | 0 | | | 0 | 0 | 8 |
| Old field | 5 | X | X | | X | X | X | X | 0 | 0 | X | X | 10 |
| Hemlock-hardwood | 1 | | 0 | X | 0 | 0 | X | X | X | | X | | 8 |
| Pine-hemlock | 1 | X | X | X | 0 | X | X | X | X | | X | | 9 |
| Scotch pine plantation | 1 | 0 | | | | X | X | | X | | X | | 5 |
| Old orchard | trace | X | 0 | | 0 | | | | | 0 | | | 4 |
| Village and farm | 9 | | | | | | | | | | | | |
| Totals | 100 | 8 | 8 | 2 | 8 | 8 | 8 | 6 | 6 | 4 | 8 | 4 | 70 |

X indicates observed feeding.
0 indicates species present but not observed to be eaten.

a. *Malus* sp. (Apple fruit)
b. *Rubus hispidus* (Dwarf raspberry)
c. *Taxus canadensis* (Ground hemlock)
d. *Gaultheria procumbens* (Wintergreen)
e. *Acer rubrum* (Red maple)
f. *Prunus serotina* (Black cherry)
g. *Tsuga canadensis* (Hemlock)
h. *Corylus rostrata* (Hazelnut)
i. *Rhus hirta* (Staghorn sumac)
j. *Quercus borealis* (Red oak)
k. *Juniperus communis* (Pasture juniper)

the percentage of the total town area occupied by each. These figures are taken from a survey of the town made in 1923 (Averill, Averill and Stevens, '23) and corrected as nearly as possible to the present.

## FIELD OBSERVATIONS

Feeding observations were made during the months from November through March in various parts of the town. All observations were made with snow on the ground and only fresh feeding was considered so there would be no confusion with the work of other animals. The general procedure was to follow tracks and note the species eaten. The greatest number of observations was made in February, followed by January and March. A total of 1,103 feeding observations were made on 62 plant species, as shown in table II. Individual tastes varied to a considerable degree. In one instance two deer traveled for some distance eating only ground hemlock. Another instance showed a deer repeatedly ignoring hazel, while others were noticeably fond of this plant.                                                    .

Calculations in the table were made on the basis of the total number of observations. An explanation of the method of counting is necessary due to the varied growth forms of the species. In tallying apple fruit, each notation in the table signifies feeding under one tree, as it was impossible to determine how many individual apples were eaten. Browsing was counted by the number of trees or small sprout clumps fed upon. Dwarf raspberry, wintergreen, and other herbaceous plants were counted as one for each patch of plants. Juniper was counted as one for each clump of bushes. The ferns were tallied as single plants. Grass was not an important factor, as the deer did not dig under the snow to get it. It was tallied as a unit wherever fed upon. It is realized that the weight given to a single sprout does not compare to that for the apples often eaten under one tree, but no better method of tallying in the available time was suggested.                               .

As can be seen from the tabulation, red maple was in this instance the most important of the browse species, followed by black cherry, white oak, red oak, and apple (see below). Of the shrubby and herbaceous species, dwarf raspberry is by far the most important, followed in order by wild raisin, hazel, and staghorn sumac. The coniferous trees most heavily browsed were Scotch pine and hemlock. The feeding on Scotch pine is probably given undue weight by many March observations in a temporary " yard " which had as its center a Scotch pine plantation. Both ground hemlock and pasture juniper are important foods, together forming ten per cent of the total feeding observations. Of these, ground hemlock was almost eight and one-half per cent. *Aspidium* followed by rock polypody was most important in the fern group, forming together 2.5 per cent of the total.

It seemed from observation borne out by comparative tallies in one cutover lot that the extent of browsing on hardwood species was proportional to

the abundance of those species in the stand where the feeding was done. Exceptions to this are noted in the following paragraph. In analyzing the types in which feeding was most prevalent, it was found that nine of the eleven most important species were eaten in the pure pine type; eight were eaten in each of the pine-hemlock and old field types; seven were eaten in the young hardwood type; five in the old hardwood and hemlock-hardwood types; four in the Scotch pine plantation type; and one in the pine-hardwood and old orchard types. To present the picture in a slightly different way, it was found that apple fruit, dwarf raspberry, red maple, black cherry, and red oak were eaten in six of the nine types; wintergreen, hemlock, and hazel were eaten in four types; while ground hemlock, staghorn sumac, and pasture juniper were eaten in only two types. In point of numbers, red maple is undoubtedly the most common tree in the region.

As was to be expected, apples were eaten as long as they were available. The percentages by months show a constant decrease as follows: November, 70 per cent; December, 5.9 per cent; January, 3.2 per cent; February, 1.5 per cent; and in March none was observed to be eaten. Apple browse was not eaten until December, when it showed as 0.4 per cent. Some species were consistently refused in feeding. *Crataegus* sp. was repeatedly ignored. Alder, *Alnus incana,* was not only ignored, but, in one case, red maple sprouts were eaten out of a clump of young alders. *Spiraea latifolia* and *S. tomentosa* were common in old fields but were never observed to be eaten. *Lyonia ligustrina,* which is less common, was also ignored.

The number of miles traveled while on the actual tracks of deer was calculated by months. These are " deer miles," *i.e.,* two deer followed one mile is recorded as two deer miles. This does not include the many miles spent in hunting for tracks or in general observations. In November 13.0 miles were recorded, in December 18.5, in January 14.5, in February 13.5, and in March 1.5. From this it can be seen that the lack of feeding observations in November was not due to the scarcity of deer. At this time the rut was still on and the bucks traveled long distances without feeding. Also, due to this factor, most of the tracks followed were made by bucks. No sure means of identifying sex by a few tracks is known, but at this season a buck was usually pawing the ground, hooking a small sapling, or fighting with another buck. Size and shape of tracks is of some help but is not conclusive and depends somewhat upon the depth and condition of the snow or ground. For this reason the obvious mating signs mentioned above were used as positive proof. Had more does been followed, more feeding might have been observed during November. During the very deep snow in March, the animals could not be located until a group was finally discovered in a Scotch pine plantation. Due to their very restricted movements mileage did not count up very fast during this time. Mileage was determined by means of notes detailing the route covered, which were later converted to distances by means of maps. For this

TABLE II. *Field observations on deer feeding*

| Species | Month of Observation | | | | | Totals | |
|---|---|---|---|---|---|---|---|
| | November | December | January | February | March | No. | % |
| | Per cent of observations | | | | | | |
| *Broad-leaved trees* | | | | | | | |
| Red maple, *Acer rubrum* | | 31.4 | 22.1 | 12.8 | 18.8 | 219 | 19.9 |
| Black cherry, *Prunus serotina* | | 3.4 | 15.7 | 4.6 | 14.6 | 90 | 8.2 |
| Apple fruit, *Malus* sp | 70.0 | 5.9 | 3.2 | 1.5 | | 39 | 3.5 |
| Apple browse, *Malus* sp | | .4 | 6.4 | 2.4 | 4.2 | 36 | 3.3 |
| White oak, *Quercus alba* | | .8 | 4.7 | 4.6 | 2.1 | 40 | 3.6 |
| Red oak, *Quercus borealis* | | 2.9 | 5.8 | 2.0 | 4.2 | 38 | 3.4 |
| Poplar, *Populus* sp | | .4 | 2.0 | 2.8 | 2.1 | 22 | 2.0 |
| Mountain maple, *Acer spicatum* | | | | 4.6 | | 21 | 1.9 |
| Hard maple, *Acer saccharum* | | | .3 | 4.1 | | 20 | 1.8 |
| Striped maple, *Acer pennsylvanicum* | | 1.3 | | 2.6 | | 15 | 1.4 |
| White ash, *Fraxinus americana* | | 2.5 | | 1.7 | | 14 | 1.3 |
| Hickory, *Hicoria ovata* | | | | 3.0 | | 14 | 1.3 |
| Chestnut, *Castanea dentata* | | .4 | 2.3 | .7 | • | 12 | 1.1 |
| Shadbush, *Amelanchier canadensis* | | 1.3 | .9 | .9 | 2.1 | 11 | 1.0 |
| Gray birch, *Betula populifolia* | | .8 | 1.2 | .4 | | 8 | .7 |
| Choke cherry, *Prunus virginiana* | | 1.3 | | .2 | 8.3 | 8 | .7 |
| Black birch, *Betula lenta* | | 1.3 | | .4 | | 5 | .5 |
| Paper birch, *Betula papyrifera* | | 1.7 | | .2 | | 5 | .5 |
| Yellow birch, *Betula lutea* | | 1.3 | | | | 3 | .3 |
| Beech, *Fagus grandifolia* | | | | .4 | | 2 | .2 |
| Cherry, *Prunus* sp | | .4 | .3 | | | 2 | .2 |
| Basswood, *Tilia glabra* | | | | .4 | | 2 | .2 |
| Hop hornbeam, *Ostrya virginiana* | | | | .2 | | 1 | .1 |
| Fire cherry, *Prunus pennsylvanica* | | .4 | | | | 1 | .1 |
| Sassafras, *Sassafras variifolium* | | | | .2 | | 1 | .1 |
| *Broad-leaved shrubs* | | | | | | | |
| Dwarf raspberry, *Rubus hispidus* | 30.0 | 22.2 | 3.5 | 1.3 | | 74 | 6.7 |
| Wild raisin, *Viburnum cassinoides* | | 1.7 | 2.9 | 4.6 | 8.3 | 39 | 3.5 |
| Wintergreen, *Gaultheria procumbens* | | 2.1 | 4.7 | | 12.5 | 27 | 2.4 |
| Hazel, *Corylus rostrata* | | | | 6.3 | 14.6 | 36 | 3.3 |
| Staghorn sumac, *Rhus hirta* | | 2.9 | 7.3 | | | 32 | 2.9 |
| Smooth sumac, *Rhus glabra* | | | 3.2 | | | 11 | 1.0 |
| Witch hazel, *Hamamelis virginiana* | | .8 | .3 | 1.5 | | 10 | .9 |
| Mountain laurel, *Kalmia latifolia* | | .8 | .6 | 1.1 | | 9 | .8 |
| Alternate leaved dogwood, *Cornus alternifolia* | | • | 2.0 | .2 | | 8 | .7 |
| Diervilla, *Diervilla lonicera* | | | | 1.7 | | 8 | .7 |
| Dogwood, *Cornus* sp | | 1.7 | | .4 | | 6 | .5 |
| Sweet fern, *Myrica asplenifolia* | | | 1.5 | .2 | | 6 | .5 |
| Viburnum, *Viburnum* sp | | | .3 | .4 | 2.1 | 4 | .4 |
| Red berried elder, *Sambucus racemosa* | | .4 | .3 | .4 | | 4 | .4 |
| Sheep laurel, *Kalmia angustifolia* | | .4 | .3 | | | 2 | .2 |

TABLE II.   (*Continued*)

| Species | Month of Observation | | | | | Totals | |
|---|---|---|---|---|---|---|---|
| | November | December | January | February | March | No. | % |
| | *Per cent of observations* | | | | | | |
| *Broad-leaved shrubs* (*Cont.*) | | | | | | | |
| High bush blueberry, *Vaccinium corymbosum*........... | | .4 | .3 | | | 2 | .2 |
| Arbutus, *Epigaea repens*...... | | | .3 | | | 1 | .1 |
| Blackberry, *Rubus alleghenien-sis*................. | | .4 | | | | 1 | .1 |
| Red raspberry, *Rubus aculeatis-simus*................. | | .4 | | | | 1 | .1 |
| Low bush blueberry, *Vaccinium pennsylvanicum*........... | | .4 | | | | 1 | .1 |
| *Coniferous trees* | | | | | | | |
| Scotch pine, *Pinus sylvestris*.... | | | | 2.8 | 4.2 | 15 | 1.4 |
| Eastern hemlock, *Tsuga canadensis*................. | | .4 | | 2.4 | | 12 | 1.1 |
| Red pine, *Pinus resinosa*....... | | | | | 2.1 | 1 | .1 |
| White pine, *Pinus strobus*...... | | .4 | | | | 1 | .1 |
| Red cedar, *Juniperus virginiana*. | | | | .2 | | 1 | .1 |
| *Coniferous shrubs* | | | | | | | |
| Ground hemlock, *Taxus canadensis*................. | | | | 20.2 | | 93 | 8.4 |
| Pasture juniper, *Juniperus communis*................. | | 1.7 | 3.5 | .4 | | 18 | 1.6 |
| *Herbs* | | | | | | | |
| Aster, *Aster* spp............. | | .4 | 1.5 | .2 | | 7 | .6 |
| Goldenrod, *Solidago* spp....... | | .8 | .9 | | | 5 | .5 |
| Grasses.................... | | .8 | | | | 2 | .2 |
| Bunchberry, *Cornus canadensis*. | | | .3 | | | 1 | .1 |
| *Ferns* | | | | | | | |
| Spiny shield, *Aspidium spinulosum*................. | | 3.4 | .9 | 1.3 | | 17 | 1.5 |
| Rock polypody, *Polypodium virginianum*............... | | | | 2.4 | | 11 | 1.0 |
| Margined shield, *Aspidium marginale*................. | | | .3 | .9 | | 5 | .5 |
| Cinnamon, *Osmunda cinnamomea*................. | | .4 | | | | 1 | .1 |
| Brake, *Pteris aquilina*......... | | | .3 | | | 1 | .1 |
| *Club mosses* | | | | | | | |
| *Lycopodium* spp............. | | .4 | | | | 1 | .1 |
| *Fungi* | | | | | | | |
| Several wood rotting species.... | | | .3 | .2 | | 2 | .2 |
| Total observations......... | 10 | 254 | 377 | 479 | 50 | 1103 | |
| Total percentages.......... | 100.0 | 101.2 | 100.4 | 99.8 | 100.2 | | 100.5 |

reason the total mileage is probably conservative, as the deer wander a great deal while feeding.  No evidence was found indicating that the deer drank from the springs and small streams remaining open while snow covered the ground.

## STOMACH ANALYSIS

To insure a more complete checking of the species fed upon by the deer and to get the quantitative relations of these foods, stomach analyses were carried out through the five months of the study.   No opportunity was available to compare this part of the study with other references, since, as far as could be discovered, no work has been done by any agency on the analysis of deer stomachs from New England.   Twenty-four stomachs were secured from within the transition forest zone of the state.   The area represented was a belt extending from Tolland and Stockbridge in the southern Berkshires eastward through Montague, Leverett, Erving, Petersham, Barre and Ware to Sterling.   It was not easy to get a large number of stomachs, as the annual kill in Massachusetts is small.   The absence of snow during the hunting season increased the difficulty of locating stomachs left where deer were dressed in the woods, because no well-defined trails were left where they were taken out.   For stomachs taken outside the legal season, game wardens were depended upon to bring in those from deer killed by dogs, automobiles, etc. This resulted in a scarcity of data, especially in January and February, as only one stomach was found in each month.   November and March had three each and December had sixteen.   The first week in December was the open hunting season.

The stomachs, after remaining in formalin for at least a week, were opened and the contents measured in quarts.   One quart was chosen as representative and kept for quantitative analysis.   The analysis technique finally developed began with washing small quantities of the material on pieces of ordinary window screen about eight inches square and held in wire frames having handles.   This separated out the very fine material.   In order to get an idea of what was in the stomach as a means of identifying fragments and to prevent any species present only as a trace from being overlooked, the so-called recognition specimens were sorted out of all the material except the quart kept for detailed analysis.   In doing this the washed material was picked over on the screens and only the specimens recognizable or capable of being identified were taken out.   Leaves of this latter class were pressed between blotters and dried for future reference.   In the case of the quart fully analyzed, the fine material washed through the screen was filtered through a piece of silk stocking to make sure no small seeds were lost.   This material was later added to the other unidentifiable remains.   In sorting over the material on the screens everything recognizable was picked out and the volume of each species measured in cubic centimeters.   The stomachs containing less than a quart had their contents converted to a quart basis for use in the percentage computations.   Any unknown specimens were sent to specialists for identification.   The average vegetable debris unclassifiable as to genus in all stomachs was 67 per cent.   Fawn stomach contents seemed to be much harder to recognize as the average unidentifiable material was 85 per cent.

TABLE III.   *Stomach analyses in volumes and percentages by months*

| | Months | | | | | Totals | |
|---|---|---|---|---|---|---|---|
| | November | December | January | February | March | Cc. | % |
| **Broad-leaved trees** | *Per cent of volumes* | | | | | | |
| Apple fruit | 85.72 | 63.94 | 90.00 | 8.51 | 3.42 | 2549 | 61.23 |
| Apple browse | | | .15 | | | 6 | .15 |
| Hardwood browse | | 6.32 | 3.73 | | 9.88 | 209 | 5.02 |
| Hard maple | | .52 | | | | 14 | .34 |
| Red oak | | .48 | | | .38 | 14 | .34 |
| Red maple | | | | | 2.66 | 7 | .17 |
| Black cherry | 1.00 | Tr.* | | | | 6 | .15 |
| White oak | | .15 | | | | 4 | .10 |
| | | | | | Totals | 2809 | 67.50 |
| **Broad-leaved shrubs** | | | | | | | |
| Wintergreen | 3.32 | 7.65 | | | 63.49 | 395 | 9.49 |
| Dwarf raspberry | 1.82 | 7.83 | | .35 | 2.28 | 231 | 5.55 |
| Sumac | .17 | 1.62 | | | | 35 | 1.08 |
| Mountain laurel | | .22 | | 2.13 | .38 | 13 | .31 |
| Wild raisin | Tr. | .15 | | | | 4 | .10 |
| Sheep laurel | | .11 | | | | 3 | .07 |
| Witch hobble, *Viburnum alnifolium* | | .04 | | | | 1 | .02 |
| Arbutus | | Tr. | | | | Tr. | |
| | | | | | Totals | 692 | 16.62 |
| **Coniferous trees** | | | | | | | |
| Eastern hemlock | | 1.69 | 4.41 | 88.65 | 1.14 | 312 | 7.49 |
| White pine | Tr. | .55 | | .35 | 2.28 | 22 | .53 |
| Pitch pine, *Pinus rigida* | | | | | 2.66 | 7 | .17 |
| Red cedar | | | | | 1.90 | 5 | .12 |
| Jack pine, *Pinus Banksiana* | | | | | Tr. | | |
| | | | | | Totals | 348 | 8.36 |
| **Coniferous shrubs** | | | | | | | |
| Ground hemlock | 1.49 | .88 | | | Tr. | 33 | .79 |
| Pasture juniper | .17 | .07 | | | | 3 | .07 |
| | | | | | Totals | 36 | .87 |
| **Herbs** | | | | | | | |
| Grasses | 1.49 | 2.24 | 1.36 | Tr. | .38 | 75 | 1.80 |
| Cabbage, *Brassica oleracea* | | .96 | | | | 26 | .62 |
| Plantain, *Plantago lanceolata* | | .85 | | | | 23 | .55 |
| False miterwort, *Tiarella cordifolia* | | .70 | | . | | 19 | .46 |
| Hawkweed, *Hieracium* sp | 2.49 | | .34 | | | 16 | .38 |
| Sorrel, *Rumex acetosella* | .66 | .36 | | | | 14 | .34 |
| Partridge berry, *Mitchella repens* | .17 | .22 | | | .38 | 8 | .19 |
| Shin leaf, *Pyrola elliptica* | Tr. | .04 | | | 1.90 | 6 | .15 |
| Red clover, *Trifolium pratense* | .50 | .04 | | | | 4 | .10 |
| Goldthread, *Coptis groenlandica* | Tr. | .04 | | | 1.14 | 4 | .10 |
| Pigweed, *Amaranthus* sp | | .07 | | | | 2 | .05 |
| Cinquefoil, *Potentilla canadensis* | .17 | | | | | 1 | .02 |
| Avens, *Geum* sp | | | Tr. | | | | |
| Ragweed, *Ambrosia artemisiifolia* | | Tr. | Tr. | | | | |
| Strawberry, *Fragaria virginiana* | | Tr. | | | Tr. | | |
| Goldenrod | | Tr. | | | | | |
| Knotweed, *Polygonum* sp | | Tr. | | | | | |
| Canada mayflower, *Maianthemum canadense* | | Tr. | | | | | |
| | | | | | Totals | 200 | 4.80 |

\* Tr. = Trace.

TABLE III. (*Continued*)

| | Months | | | | | Totals | |
|---|---|---|---|---|---|---|---|
| | Novem-ber | Decem-ber | Jan-uary | Febru-ary | March | Cc. | % |
| *Ferns* | Per cent of volumes | | | | | | |
| Spiny shield.................... | .33 | .19 | | | | 6 | .15 |
| Rock polypody................ | Tr. | | | | | | |
| Christmas, *Polystichum acrosti-* | | | | | | | |
| *choides*...................... | | | | | Tr. | | |
| Cinnamon.................... | | Tr. | | | | | |
| Brake....................... | | Tr. | | | | | |
| | | | | Totals | | 6 | .15 |
| *Club mosses* | | | | | | | |
| *Lycopodium obscurum*........... | | .07 | | | | 2 | .05 |
| *Lycopodium complanatum*........ | | .04 | | | | 1 | .02 |
| | | | | Totals | | 3 | .07 |
| *Mosses* | | | | | | | |
| Sphagnum, *Sphagnum* sp........ | | | | | Tr. | | |
| Polytrichum moss, *Polytrichum* sp. | | Tr. | | | | | |
| *Fungi* | | | | | | | |
| *Panus stipticus* | | | | | | | |
| *Polyporus elegans* | | | | | | | |
| *Daedalia confragosa* ........... | .50 | 1.91 | | Tr. | 4.56 | 67 | 1.61 |
| *Stereum rameale* | | | | | | | |
| *Scleroderma vulgare* | | | | | | | |
| *Lichen* | | | | | | | |
| Unidentified.................... | | | | | .38 | 1 | .02 |
| *Grand totals* | | | | | | | |
| Per cent..................... | 100.00 | 99.95 | 99.99 | 99.99 | 99.97 | | 100.43 |
| Cu. cm....................... | 603 | 2719 | 295 | 282 | 263 | 4162 | |

As shown in table III, a total minimum of 57 species was found in the stomachs. Apple fruit formed 61 per cent of the total volume. Wintergreen, hemlock and dwarf raspberry were next in order with 9, 7, and 5 per cent respectively. By groups, the hardwood trees composed 67 per cent of the total volume, broadleaved shrubs 16 per cent and coniferous trees 8 per cent.

As a monthly average, apple fruit decreased rapidly after January, which appears most logical as the apples are apt to be decomposed or buried under the snow. Unless the snow is too deep, the deer will go to some trouble to dig down to reach them. From December on, the stomachs showed a much higher percentage of hardwood twig and stem material than the earlier ones. The coniferous trees show the same trend. Dwarf raspberry diminishes in amount with increasing depth of snow. Wintergreen shows heavy feeding in March, but most of it came from one stomach. Probably this animal found an exposed patch of the plant and made its last meal on it.

Perhaps the most unusual thing brought out by this study was the amount of fungi eaten, 1.6 per cent of the total. It showed an increasing trend

TABLE IV.  *Rating of most important plants in preference by months.  Based on a combination of field observations and stomach analyses*

| November | December | January | February | March |
|----------|----------|---------|----------|-------|
| Foods in order of importance | | | | |
| 1. Apple | 1. Apple | 1. Apple | 1. Hemlock | 1. Wintergreen |
| 2. Wintergreen | 2. Red maple | 2. Red maple | 2. Red maple | 2. Red maple |
| 3. Dwarf rasp- | 3. Dwarf rasp- | 3. Staghorn | 3. Apple | 3. Unidentified |
| berry | berry | sumac | 4. Hazelnut | hardwood |
| 4. Ground hem- | 4. Wintergreen | 4. Hemlock | 5. Mountain | 4. Black cherry |
| lock | 5. Unidentified | 5. Red oak | laurel | 5. Hazel |
| 5. ——— | hardwoods | | | |

from November to March. The species were largely the woody or corky varieties. These are found on dead or fallen trees and on stumps. Five species of fungi were found in a total of ten stomachs.

Some oddities which cannot be explained except as accidental were chips of wood in three stomachs, a grasshopper wing, a feather, two kinds of insect larvae, a stone one-fourth inch in diameter, several small bright quartz pebbles, and several wadded balls of the animal's own hair. With the exception of the hair, these were probably picked up in ground feeding.

## BEDDING

During the whole period of observation the deer showed a strong preference in bedding habits for coniferous forest types. A total of 86 beds were observed, of which 39, or nearly one-half, were in natural white pine stands 15 to 70 years of age. Eighteen, or slightly less than one-fourth were in a Scotch pine plantation, which, for bedding, was essentially the same as the younger white pine stands. Only seven of the total were in hardwood stands or in the open. It appeared that only day beds were found here. This is undoubtedly due to the warmth of the sun's rays in these locations. Day beds in coniferous stands were often on the north side of openings where the sunshine reached the ground.

Usually the beds were placed where the lowest coniferous limbs were from five to ten feet above the ground. There appears to be no attempt on the part of the animal to locate beds where there is any particular degree of visibility. The ears and nose rather than the eyes are apparently relied on to warn the animal of danger. There seems to be no marked preference for bedding on a particular slope. The gradual west slope seemed to be used more than any other, but most of the town has a gradual west slope, so this factor would not appear to be significant. The beds were usually made on knolls rather than in depressions.

TABLE V. *Rating of plants in preference as winter deer food. Based on stomach analyses, feeding observations and judgment of the authors. The species listed as "very important" are ranked in order; but, within the other groups, no effort was made to rate the species*

*Very Important*

1. Apple fruit
2. Dwarf raspberry
3. Ground hemlock
4. Wintergreen
5. Red maple

6. Black cherry
7. Hemlock
8. Hazel
9. Staghorn sumac
10. Red oak

11. Pasture juniper

*Important*

White oak
Poplar
Mountain maple
Striped maple
Hard maple
Apple browse
Wild raisin

White ash
Hickory
Chestnut
Shadbush
Black birch
Yellow birch
Witch hazel

Dogwood

Mountain laurel

Sorrel

Spiny shield fern

Partridge berry
.

Fungi

*Occasionally Eaten*

Gray birch .
Paper birch
Choke cherry
Fire cherry
Bush honeysuckle
Sweet fern
Viburnum
Witch hobble
Arbutus
Highbush blueberry
White pine
Scotch pine

Beech
Escaped cherry
Sassafras
Basswood
Poison elder
Willow
Blackberry
Red raspberry
Lowbush blueberry
Smooth sumac
Pitch pine
Red pine

Red cedar

Sheep laurel

Grasses
Aster
Goldenrod
Bunchberry
Rock polypody
Flowering fern

Shin leaf
Red clover
Goldthread
Five-finger
Margined shield fern
Brake fern

Christmas fern

Club moss

*Rarely Eaten*

(Includes several species found only as "recognition specimens" in stomachs)
Speckled alder, *Alnus incana*
Snowberry, *Symphoricarpus racemosus*

Jack pine

Cabbage
Plantain
Hawkweed
Pigweed
Avens
Ragweed
Polytrichum moss

Canada mayflower
Strawberry
Speedwell, *Veronica officinalis*
Knotweed
Pinweed, *Lechea* sp.
False miterwort
Sphagnum moss

Lichen—species unknown

## DEER HABITAT CHANGE

The deer habitat change was very marked in the vicinity of Petersham during the winter. With the fall of the first snow, an effort was made to locate, as nearly as possible, the locality occupied by each small group of deer. During late October and early November when the deer were in the rutting period, they were constantly shifting. With the snows of early December they became rather localized in movement, and it was not difficult to find the local range. At this time, about 23 deer in seven groups, or one to approximately 200 acres, were located and usually observed several times. They appeared to be settled for the winter until the bitter cold weather and deep snows of late December occurred. Groups which had not moved out of an area of 40 or 50 acres during the early part of the month shifted, and for some time no trace of any of them could be found. In the middle of January two deer were found in the southern part of the town, but nightfall and a heavy snow during the night prevented tracking to note their movements. They had been in a thick pine-hemlock stand which bordered a pine cutting of three years previous. The locality in which they were found gave some clue as to the type of cover which they desired at this time of the year. Shortly afterward a trip was made to the town of Erving where a herd of 15 to 20 deer were using Rattlesnake Mountain as their winter range. Dogs were harassing this herd to a considerable degree, and yet they did not move, which led to the belief that such an area was very favorable to the herd under the weather conditions prevalent during the winter. The range was mainly on south and southeast slopes and was covered with young hardwood and occasional clumps of pine and hemlock.

Upon returning to Petersham an area was sought with the features apparently desired. Such a one was found in the southwest part of the town where precipitous ledges on the south and east sides of numerous short parallel ridges gave the proper topography and aspect. The cover was largely pine and hemlock with an admixture of hardwoods. A number of deer were found in this region, the total being about ten. In an effort to secure as much data as possible relative to feeding, these deer were apparently pursued too closely, as they promptly moved. Not until early March when the snow was about two feet deep were any found again, and these were discovered about a mile south of the original point in a fifteen-year-old Scotch pine plantation. Three deer stayed here in an area of about two and one-half acres for at least a week, making the nearest approach to a yard which was observed. Whether they were members of the same group could only be conjectured. Soon after these deer were found, the March thaws set in, making human travel next to impossible and putting an end to observations in the woods.

Since the last tracks seen in several places after the first heavy snowfall headed south and the natural drainage of the town is down the Swift River Valley in that direction, it is presumed that the deer drifted on to the south

with the advent of cold weather; but no field observations were made beyond the town. During early April several deer tracks were noted on the cut-over area mentioned above as the last place where the deer were found in early December. Later observations and conversations with local people indicated that the animals were again back in the early winter ranges by late spring. In order to prove conclusively the deer habitat shift in the town, they would have to be followed over several seasons. It is also likely that they would not shift so far in a milder winter.

## Ways in Which Forestry can be Expected to Improve Deer Range in the Region

This study indicates several ways in which forestry can create conditions favorable to the deer in this region. Mixed stands or small areas of hardwoods and softwoods interspersed furnish the variety necessary for food and cover. Apparently fairly dense coniferous stands in protected situations are necessary to hold a herd in a given locality during a severe winter. Planting of conifers with spacings six by six feet may create suitable cover by an age of fifteen years. These plantings should not be in extensive blocks, since they will constitute a practical desert for many years as far as game food is concerned. As these stands get older, thinnings allow more hardwood advance growth to come in, thus increasing the amount of winter deer food available. In young hardwood stands or in coniferous plantations on cut-over land, weeding to improve composition and form of the crop trees produces an abundance of the young sprouts on which the deer so largely depend during winter. The importance of the usual three weedings necessary to develop a satisfactory young stand on cut-over land and which result in young sprouts available over a period of ten to fifteen years can easily be seen. Hardwood sprouts in dense stands which are not weeded normally pass the point of furnishing much in the way of browse for deer in from six to ten years. Also, the creation of a wealth of young, tender sprouts tends to attract the deer away from the crop trees which are more difficult to reach and apparently less palatable. Sustained yield management of a given tract results in periodic cuttings which can be distributed over the area in such a way as to furnish the requisite interspersion of age classes for good deer range. Thrifty apple trees should be favored in weedings and thinnings. Fire line and road margins sown to clover or other plants relished by the deer can furnish abundant summer and fall food.

## Summary

1. The study was made between November, 1933 and March, 1934 mainly in the town of Petersham which lies in the transition forest region of north-central Massachusetts.

2. The winter covered by the study was one of the most severe known in the region. Temperatures down to — 35° F. were recorded in the town and

the November–March snowfall was 87.75 inches compared to the past ten year average of 52.25 inches. The ground was snow covered from early December until late March.

3. Descriptions are given for nine cover types used by the deer during the winter and table I summarizes the more important deer foods present in each.

4. A total of 1,103 feeding observations were made on 62 plant species.

5. Individual tastes among the animals were found to vary widely.

6. Among the broad leaved trees red maple was the most important food species taken followed by black cherry, white oak, red oak and apple. Of the shrubs and herbaceous species dwarf raspberry was most used followed by wild raisin, hazel and staghorn sumac. The coniferous trees most heavily browsed were Scotch pine and hemlock that in Scotch pine being influenced by the presence of partial yarding of animals in a plantation of this species. Ground hemlock and pasture juniper were important also. *Aspidium* and rock polypody were most important in the fern group.

7. The extent of browsing on hardwood species seemed, in general, to be proportional to the abundance of these species in the stand where the feeding was done.

8. Of the eleven most important species observed to be eaten nine were found in the pure pine type, eight each in the pine-hemlock and old field types, seven in young hardwood, five each in old hardwood and hemlock-hardwood, four in the Scotch pine plantation and one each in the pine-hardwood and old orchard types.

9. Apple fruit was eaten whenever available decreasing from 70 per cent of the feeding observations in November to 1.5 per cent in February.

10. Species ignored in feeding were *Crataegus* spp., *Alnus incana, Spiraea latifolia, Spiraea tomentosa* and *Lyonia ligustrina.*

11. Twenty-four deer stomachs were collected between November and March from the transition forest region of central and western Massachusetts and their contents analyzed. Analysis methods are described.

12. A total of 57 species were identified from the stomachs. Apple fruit formed 61 per cent of the total food volume. Wintergreen, hemlock and dwarf raspberry were next in order. Hardwood tree species including apple produced 67 per cent of the total volume, broad leaved shrubs 16 per cent and coniferous trees 8 per cent.

13. The amount of apple fruit in the stomachs decreased rapidly after January while the amount of hardwood and coniferous browse increased after December.

14. A monthly rating of the five most important winter foods is given.

15. Wood rotting fungi formed 1.6 per cent of the total stomach contents.

16. Based on all the information available from the study, a rating of plants in preference as winter food was made separating them into four groups.

17. During the winter the deer showed a very strong preference for coniferous types for their beds.

18. The deer in the town shifted their habitat with the onset of deep snow and severe cold, but no real yards were found.

19. From the standpoint of deer, mixed stands or good interspersion of conifers and hardwoods are most desirable.

20. Thinnings, weedings and periodic cuttings produce a wealth of winter deer food in the locality studied.

21. Apple trees should be left to produce food for the deer wherever possible.

## Acknowledgments

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# ROOT SYSTEMS OF WOODY PLANTS OF OLD FIELDS OF INDIANA

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The root habits of plants of various environments have been investigated by different workers but no one seems to have examined those of a group of woody species which occur very frequently in old fields in southern Indiana. A study of the root systems of the woody plants of such communities seems, therefore, to have promise of interesting and valuable results.

In Europe root studies have been attacked rather vigorously. Büsgen and Münch ('29) give an excellent summary of the work done. In this country Cannon ('11) made a thorough study of the roots of desert plants. Weaver ('19) gave another valuable contribution to our knowledge of roots. Weaver and Kramer ('32) described the invasion of trees into grassland in eastern Nebraska. The dry prairie is slowly invaded by shrubs, the three principal species concerned being smooth sumac, *Rhus glabra,* coralberry, *Symphoricarpos orbiculatus,* and hazelnut, *Corylus americana.*

Cannon ('11) grouped roots into three types: (1) generalized, with tap root and laterals both well developed; and the specialized; (2) those with prominent tap roots; and (3) those with prominent laterals. This grouping is used in the descriptions of root types in this paper.

Formerly almost all of southern Indiana was in deciduous forest. Now few old-age forests are present. After clearing, cultivation of a field results in exclusion of most species formerly present. Later if a field becomes poorer due to inefficient management, it loses much of its usefulness. Cleared places are very often turned into pasture or abandoned entirely.

Usually the fields are slowly invaded by species such as *Rhus copallina,*[1] *Sassafras officinale, Smilax rotundifolia,* and *Symphoricarpos orbiculatus.* They are more able to establish themselves than those of the natural assemblage of more mesophytic woodland plants. It was in this latter group of shrubby species in which the investigations of root habit were made.

## CLIMATE AND SOILS

The growing season around Bloomington, Indiana, near which the present investigations were made, is about 170 days. The average annual precipitation is about 40 inches, each month usually receiving 3 inches or more. The dry months rarely fall below 2.5 inches. A little over fifty per cent of the

[1] Nomenclature follows Deam ('29), ('31), and ('32).

rain falls in the warmer six months, April to September.  Growth water is present in the soils at nearly all times, though wilting occurs after long periods of drought.  These droughts are rarely so severe as to produce permanent wilting.  The soils are free from glacial deposits, and consist largely of limy and sandy clays or a mixture of both.  In winter they are loosened by repeated freezing and thawing.

## INVESTIGATION

The method employed in excavating the root systems was similar to that employed by Weaver ('19).  A trench was dug by the side of the plant to be examined.  The soil was carefully removed from the side of the trench exposing the roots.  Several roots of a given species were examined and then a working description of the root system was written.  A typical root aggregation was chosen and drawings of horizontal and vertical distribution were made to scale at the time of excavation.

Root systems of *Rhus copallina, Rosa setigera, Rubus allegheniensis, Populus grandidentata, Sassafras officinale, Symphoricarpos orbiculatus,* and *Smilax rotundifolia* were investigated.  These plants were all invaders of areas otherwise free from woody species.  They were found to have efficient means of vegetative propagation, and all possessed well developed systems of absorbing organs.  All the roots were more shallow than those of the deep rooted species of the prairies described by Weaver ('32).  There was no indication of conditions which would result in the formation of shallow roots due to physiological conditions of any sort.

Each species of plant is considered separately.

### *Rhus copallina* L.

The shining or winged sumac, is very common especially in old abandoned fields, along borders of woodlands, and along fences and roadsides.  It is an erect shrub generally 1 to 2.5 meters high.  The roots are of the specialized type with prominent laterals.  It propagates largely by means of its long rhizomatous roots, which send up numerous shoots.  One continuous root, 16.6 meters long, was excavated.  The course taken by such a root often can be traced by a series of erect shoots.  These laterals, rarely penetrating deeper than 15 cm., form a very extensive system.  Figure 1 shows a connected system about twelve meters across, consisting of five shoots none of which is over one meter high.

On all the branch roots are numerous short fine branchlets which in many places form a fibrous mat (fig. 3).  Such a mass of roots enables the plant to invade an area and to compete successfully with the grasses.  The shoots from the vast network of lateral roots finally coalesce into a closed canopy above the grasses which ultimately disappear as a result of increased root competition and shading.
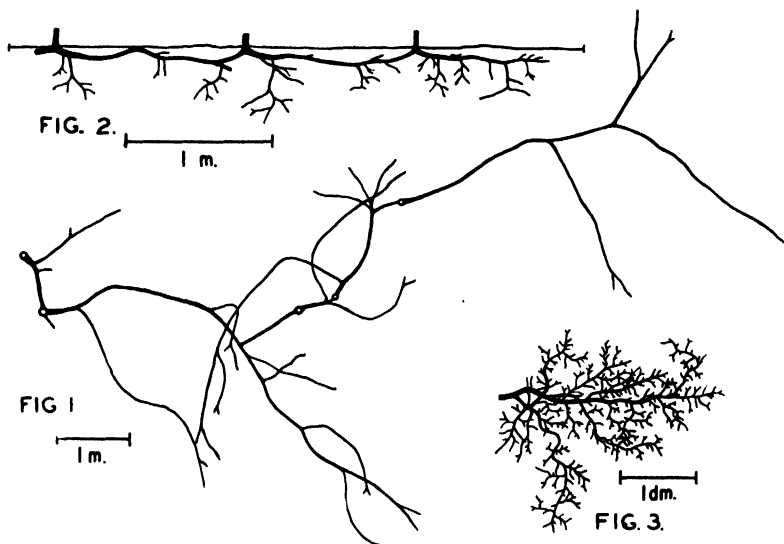
FIG. 1. Horizontal distribution of main lateral roots of *Rhus copallina* from a hilltop in the Morgan-Monroe Forest, showing five shoots.

FIG. 2. Vertical distribution of roots of *Rhus copallina* on a lateral on which there were three shoots.

FIG. 3. Mass of roots at the tip of one of the smaller branching roots of the plant shown in figure 1.

Detailed data for the system of five shoots shown in figure 1 are given in table I where the shoots are taken in order of increasing distance from the parent plant. There was an increase in the diameter of the main lateral immediately after each shoot. A vertical root was present just beyond each shoot (fig. 2).[2] The shoots seemed to have come from points at which the main lateral had risen to near the surface of the ground. In a system of three shoots, 7, 6, and 4 years old respectively (fig. 2), the main lateral at the 7-year shoot was at the soil level, then it dipped down to a depth of 7 cm., and up to within 1 cm. of the surface in a total distance of 53 cm. At that

TABLE I. *Measurements in centimeters of connected shoots of Rhus copallina. Diameter just above basal swelling*

|  |  |  | Diameter of main lateral root | |
|  |  |  | Before shoot | After shoot |
| Age | Diameter | Height | | |
|---|---|---|---|---|
| 11 | 2.0 | 100 | 1.3 | 2.5 |
| 10 | 2.0 | 90 | 1.3 | 2.0 |
| 7 | 1.5 | 95 | .8 | 1.5 |
| 7 | 2.0 | 95 | .8 | 1.8 |
| 2 | .5 | 60 | .9 | 1.0 |

[2] Taken from a different location but of similar habitat.

point there had been a sprout, now dead. This sprout had caused a noticeable swelling of the main lateral from 12 to 14 mm. in diameter. The 6-year old shoot 75 cm. away arose just 3 cm. below the surface of the ground, the greatest depth of the lateral in that section being 10 cm. and its diameter preceding the shoot 12 mm. The diameter increased to 19 mm. after the shoot, then ran along for 115 cm. with a maximum depth of 13 cm., to the 4-year old shoot. Here the main lateral swelled from 10 to 16 mm. in diameter, and extended on for 90 cm. branching very profusely. Here again roots were present just beyond each sprout. In this case the maximum depth of any root was 55 cm.

Excavations of other individuals indicated that most of the root systems are within the top 35 cm. of the soil. Roots of larger and older individuals were discovered to have penetrated as deep as 1.42 meters. However, *Rhus copallina* in the zones where it is advancing on the old fields, that is, on the outer extremities of systems such as described, most assuredly is dependent on shallow roots.

Radial transects were made of a number of clumps of the sumac. The ages of the shoots were found to increase gradually toward the center of the clumps. Zones representing different ages were established and the average rate of spread determined.

Three habitats apparently differing in degree of xeric conditions gave rates of spread ·as follows: (1) A rather poor, dry hill in the Morgan-Monroe Forest, 5.4 m. in 9 years or 60.0 cm. per year; (2) A somewhat richer hilltop in Brown County, 9 m. in 12 years, or 75.0 cm. per year; and (3) A rather moist hillside three miles northeast of Bloomington, 7.5 m. in 9 years, or 83.3 cm. per year. Extensive studies of relations existing over a long period of time are needed to establish just what influences the rate of spread.

### Rosa setigera Michaux

This species is commonly associated with open places and is often found in old pastures. It is a widely spreading shrub, the stems usually 1.5 to 4 m. long. In the open it is found alone or associated with *Rhus, Smilax,* and *Rubus.* It propagates by means of seed and by rooting at the tips of its long arched branches. No new plants sprouting from roots were found.

The root system is plastic and does not possess a constant form in the area studied. No plants whose roots were examined were specialized to the extent of possessing a prominent tap root. The majority had a rather pronounced development of lateral roots. Thus, the plant falls into the specialized type with a prominent lateral root system.

The roots of two plants will represent the extremes of root types present here. The first was one with the laterals most prominent (fig. 4). It was chosen from a number of scattered individuals growing near the top of a grassy hillside. There were seven lateral roots. At one decimeter from

the crown they were 1.2, 1.1, 1.0, 0.8, 0.6, 0.5, and 0.3 cm. in diameter.    In the order mentioned above they extended almost horizontally 95, 135, 110, 88, 115, 97, and 81 cm. from the crown, measured in a straight line, their tips were 10 to 39 cm. from the soil surface.    Numerous profusely branched secondary roots extended horizontally from the main laterals, most of them from 1.5 to 3.0 mm. in diameter.    Numerous laterals took a course straight downward, only slightly oblique, as far as 32 cm. from the main lateral, with a maximum root depth of 64 cm. giving a very shallow root system.
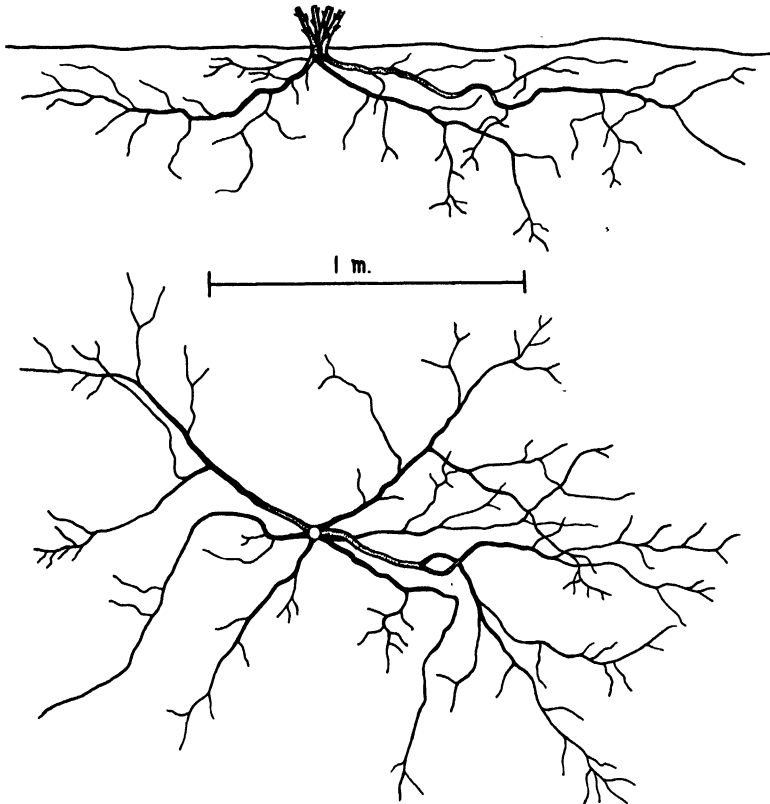


FIG. 4.    Vertical and horizontal distribution of roots of a plant of *Rosa setigera* with a prominent lateral type of root.

A specimen with five main laterals and a tap root will illustrate the other extreme of root type (fig. 5).    It grew in an old pasture on the flat top of a hill in Brown County on soil derived from Borden rock.    The laterals were similar to those of the first plant described, although somewhat thinner.    The tap root, the deepest of any found, extended to a depth of 1.57 meters.    Numerous secondary laterals extended horizontally from the tap root.    Most of them were under 3 mm. in diameter, three being just over 3 mm.    The

three largest laterals were 80, 65, and 35 cm. long.   Numerous rootlets up to 5 cm. long were found throughout the system, forming a fine network.

### *Rubus allegheniensis* Porter

This species found in all parts of Indiana, grows best in moist, rich soil in cut-over and open woodlands, along fences, roadsides, and in similar situations.   It is also found in open fields where it sometimes forms almost impenetrable thickets about a meter high.   The canes are biennial, but the roots are perennial with a large number of branching laterals, rhizomatous in habit which penetrate the soil thoroughly.
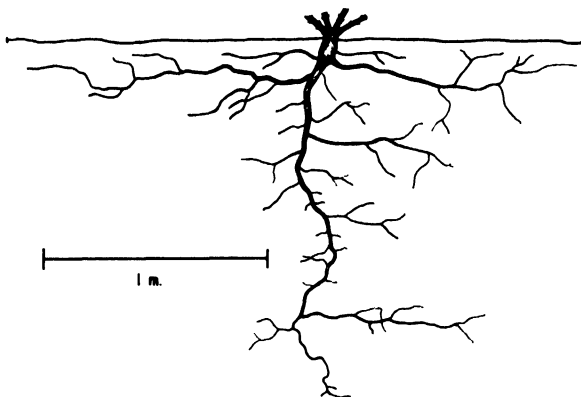


FIG. 5.   Vertical distribution of roots of a plant of *Rosa setigera* with well developed tap root and laterals.

Figure 6 is typical of a vertical transect of the roots of this blackberry. The main laterals are largely in the top 20 cm. of the soil although sometimes they dip as low as 27 cm.   The first canes arise from the superficial laterals at a depth not greater than 7 cm.   The subsequent canes arise mostly at the base of the first cane, forming the crown.   Numerous fine roots, about 2 mm. in diameter, radiate from this crown, few of them exceeding 35 cm. in length.

The deepest roots penetrate to 103 cm., although few go below 80 cm. They originate from various places on the main laterals and usually, but not always, from under the crowns of the canes.   All of the roots become very finely divided, penetrating almost every part of the soil and are thus usually able to compete successfully with other plants with which they are associated.

### *Populus grandidentata* Michaux

This species is a small to medium sized tree, 10 to 40 centimeters in diameter.   In southern Indiana it grows on the tops and sides of hills and is

rarely found in low ground. Reproduction is largely dependent upon the abundant root suckers, more than sufficient to form a stand, many of them being eventually crowded out. Several suckers were found over 10 m. from parent tree, and one was 13.1 m. away.

Fig. 6. Vertical transect of the root habit typical of *Rubus alleghaniensis*.

The root system consists of a number of radiating shallow roots with numerous vertical and horizontal feeding branches (fig. 7). These feeding roots do not occupy the soil as thoroughly as do those of *Rhus copallina*. The main lateral roots which are rhizomatous in habit, are seemingly devoted to reproduction. They are rarely deeper than 30 cm., but often rise and fall, shoots developing where they approach the surface of the soil. When a sprout forms on a root, a thickening takes place near the point of attachment, especially on the side toward the tip where many feeding rootlets develop. The vertical roots are rather shallow. Near a 6-year old sucker one was found to penetrate to a depth of 1.2 m.

Very few, if any, feeding rootlets formed due to the presence of a sucker, occur between it and the roots arising near the preceding sucker. Few cases were found in which feeding roots arose immediately at the sucker.

Examples of rates of spread determined by radial transects are as follows:
(1) 9.8 m. in 10 years, on a hillside 10 miles southeast of Bloomington;
(2) 10.8 m. in 13 years, in poor soil on hilltop 12 miles northeast of Bloomington; and (3) 12.8 m. in 10 years, on a hillside in Morgan-Monroe State
Forest.
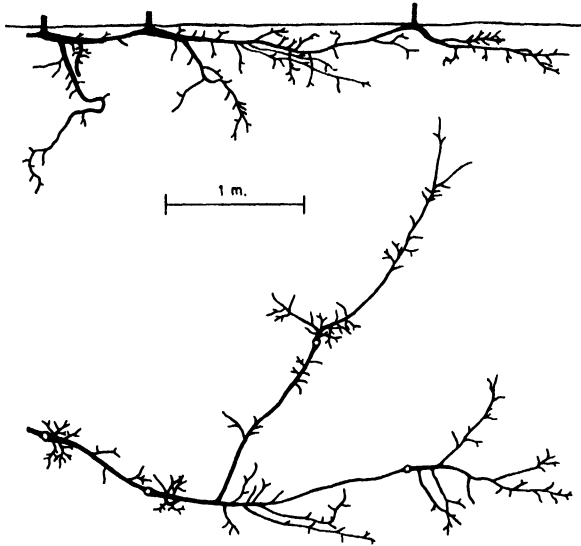


Fɪɢ. 7. Vertical and horizontal distribution of a lateral root of *Populus grandidentata*. The lateral was one from a 15-year old tree, the drawing including the portion 3.7 meters from the tree to the tip.

### *Sassafras officinale* Nees & Ebermaier

This species is a small tree, in southern Indiana, found mostly on the tops of ridges, in almost all kinds of soil, often becoming a pernicious weed tree. It invades fence rows, pastures, and fallow fields, and once established is extremely difficult to eradicate. If cut down, a large number of root suckers and stump sprouts will develop and when the roots are severed in plowing or grubbing, every piece of root is likely to send up a sprout. Even-aged thickets of sassafras often arise when a cultivated field full of roots and supressed shoots is allowed to lie fallow. In old pastures biotic influences usually keep the trees in clumps but they soon spread by means of root suckers as grazing is stopped. Several spreading clumps in different situations were investigated and the rates of spread determined. They ranged as high as 94 cm. per year over a period of 12 years with a mean average of 73 cm. per year.

The sassafras roots were found to be of the prominent lateral type (figs. 8 and 9). The long laterals extend for a distance with very little change in diameter, branching occasionally, and forming an increasingly complex sys-

tem. These roots alone result in an extensive network, in addition to which there are numerous smaller roots. The laterals are practically all from 15 to 50 cm. deep, rising and falling at various intervals.

The root suckers cause enlargement on the roots at the place of attachment, especially towards the root tip. For example, in figure 9 the diameter of the root at the 5-year old tree on the side next to the parent tree is 9 mm., measured 5 cm. from the crown. At 5 cm. distance on the other side the diameter is 26 mm. At the 4-year old shoot the diameters are 11 and 24 mm. respectively, and at the 1-year old, 5 and 7 mm.
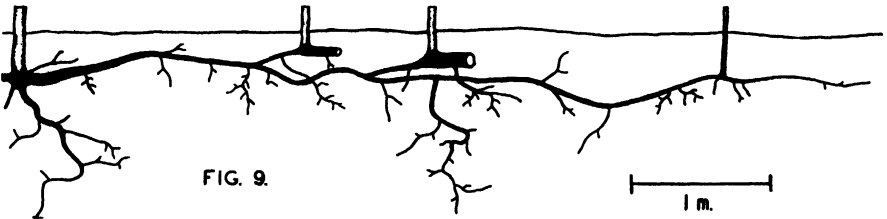


Fig. 8. Horizontal distribution of roots of *Sassafras officinale* in an area of one by six meters on the edge of a clump invading an old field.

Fig. 9. Vertical distribution of roots shown in figure 8 with 7-, 5-, 4-, and 1-year old suckers.

The forming of a sucker results in the development of feeding roots that otherwise would not be present on the lateral. These roots arise near the sucker and on the larger part of the lateral. Occasionally a prominent feeding root is found attached directly to the base of the sucker but others, just as important, are almost always found a short distance from the sucker. These feeding roots branch to very fine rootlets which most certainly are very important in the plant's adaptability to vigorous growth in the various types of soil.

*Symphoricarpos orbiculatus* Moench

This species, commonly called coralberry, is a very abundant shrub in certain hilly localities in southern Indiana. It grows from .5 to 1.5 m. in height, largely in clumps due to its vegetative propagation. Deam ('32) states that it is usually found in open sunlight and that in open woodlands it often becomes so thick as to ruin them for pasture. It produces numerous stolons or runners which sprout and root at intervals in their course over

the surface of the ground, extending the area occupied by the species. A single runner was found that had gone 2.4 m. in one year. Weaver and Kramer ('32) have found that *Symphoricarpos symphoricarpos* (L.) MacM. (*S. orbiculatus* Moench) in eastern Nebraska spreads underground by rhizomes and above ground by runners, the latter playing a less effective part. It is very strange that in all of the places investigated in southern Indiana not one plant was found that had its origin from a rhizome.

One hundred and fifty different groups, consisting of an original plant and its surrounding offspring, were investigated. When the members of a group were vegetatively connected, they were found to have arisen only from above ground runners. Often these runners were on the surface of the ground or lightly covered by soil. In grassy habitats they were usually hidden beneath the grass and sometimes beneath the accumulated litter. The explanation of this difference in propagation between the region studied by Weaver and this one might lie in the rhizomes being more effective propagators in the more xeric habitat. Possibly a detailed study and transplant experiments would prove this distinct difference to be permanent.
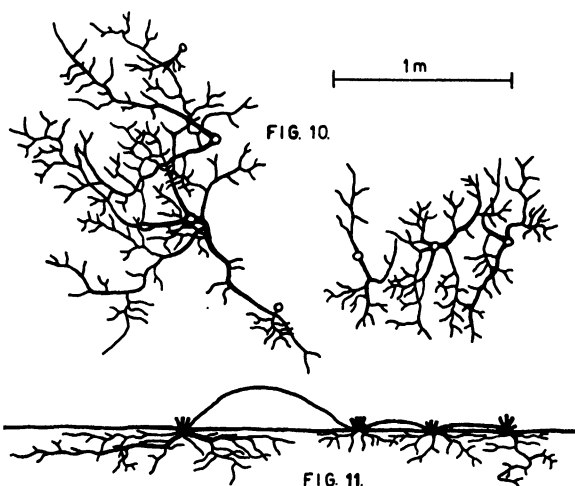


FIG. 10. Horizontal root distribution of a group of plants of *Symphoricarpos* connected vegetatively by means of runners. From an old field on hilltop in Lawrence County.

FIG. 11. Vertical distribution in a transect through the root systems in figure 10, showing the connecting runners.

The root systems of an isolated group of plants were excavated and carefully plotted (figs. 10 and 11). They had all arisen from runners that came from the original plant which was nine years old and had three main roots. One was 11 mm. in diameter and the others 9 and 7 mm. They extended horizontally, branching into a fine network, the whole mass having a

gnarled appearance. The lateral extent of the three roots were 110, 116, and 77 cm., respectively. Generally the roots are shallow, in this case reaching a depth of 33 cm. (fig. 11). One large plant from another habitat was found to have roots penetrating to a depth of 118 cm.

A 3-year and a 1-year old sprout will serve well to indicate the root growth of the sprouts. At the 1-year plant there was one root 32 cm. long. It was adventitious on the runner and ran obliquely downward to the tip at a depth of 21 cm. In the 3-year old (typical for the younger ages) there were three main roots. They extended out 50, 54, and 65 cm., and to the depths of 21, 11, and 17 cm. at the tips. On the first root indicated, 16 cm. from the crown, a branch threaded its way downward to a depth of 33 cm.

## Smilax rotundifolia L.

This species is a large climbing vine with long underground stems. The vines are 5 to 10 mm. in diameter and are covered with spines often forming impenetrable tangles. Once established the plant spreads by means of numerous branching rhizomes which send up shoots at various intervals. Smilax is found in old fields, along fences and roadsides, in open woods, and is especially common in old pastures.
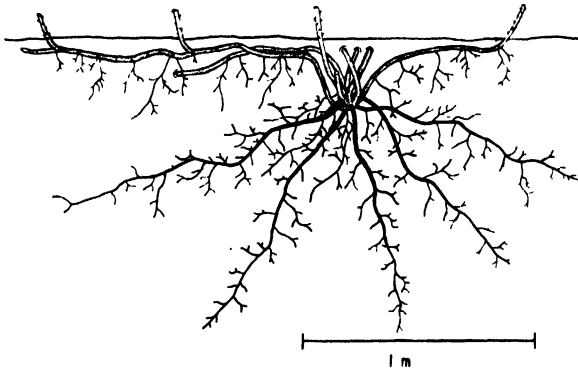


FIG. 12. Vertical transect through mass of rhizomes and radiating roots of Smilax rotundifolia. Plant was in an old pasture.

The underground systems consist largely of a number of rhizomes and adventitious roots, which tend to radiate from a central mass (fig. 12). The adventitious roots, the aerial stems, and branches of the rhizome originate from nodes of the rhizomes. The rhizomes are usually between 7 and 12 mm. in diameter, running along near the surface of the ground, rarely deeper than 15 cm. The tips sometimes arch to the surface and form aerial shoots. More often the shoots are formed from short branches of the rhizomes. It was found that new rhizomes originate from the central mass each year, the first node of each new rhizome sending out feeding roots that radiate in all

directions (fig. 12). These roots are from 1 to 2 mm. in diameter and run in a rather straight course. They send off numerous rootlets, from 5 to 30 cm. in length. The roots usually penetrate to about a meter in depth but reach as deep as 1.5 m. The root systems penetrate the soil quite thoroughly but were not as finely divided as the other species investigated.

## DISCUSSION

The most striking feature of the root system of the species studied is their lateral spread, the roots being all relatively shallow when compared with species of similar type and stature described by Weaver ('32). In *Rhus copallina* most of the roots are within the top 35 cm. of the soil. In the center of the clumps where the plants are older and larger the roots penetrate as much as 1.42 m. It appears that water and nutrients are received by the younger individuals through the connecting laterals. However, individuals with laterals that had been severed several years previously did not seem to have developed roots much deeper than those of individuals still connected to the parent plant. The same is true of *Populus grandidentata* and *Sassafras officinale*.

All of the species investigated possess efficient means of vegetative propagation, either above ground by runners or underground by rhizomes or sprouts from roots. In many of the old fields one method of propagation is just as efficient as the other. However, in the drier fields it appears that above-ground runners are less effective. For example, runners of *Symphoricarpos orbiculatus* in dry fields are found to be rooted at less frequent intervals than those in a more mesophytic habitat. It is evident that runners on the ground have more difficulty in rooting on dry soil than do those structures under the soil surface.

The type of root system of each species is noticeably constant with the exception of *Rosa setigera*. Just what specific conditions caused the variations in *Rosa setigera* from the shallow type with prominent laterals to that of prominent tap root were not determined. Holch ('31) stated that the type of root appears to be a hereditary adaptation of the species to sites of more or less specific water content. Markle ('17) stated the two important factors in root distribution were moisture content of the soil and its penetrability.

The average rates of vegetative spread of the various species are slow but represent a fairly rapid growth of the parts from which the new individuals arose. Sassafras and sumac average 73 cm.. and aspen 103 cm. per year. All three propagate from underground roots. It can be seen that this seemingly slow invasion of a new area by means of sprouts from underground roots is a remarkable accomplishment. It is slow, but the result is sure. It appears that the successful invasion by all the species studied is due to their efficient root systems which are able to compete for water and nutri-

ents with other species present. As the canopy of shrubs increases, the grasses are crowded out. Then, later on, trees are able to establish themselves as a result of the more mesic conditions brought about by the shrubs. It can readily be seen that a knowledge of root distribution of the woody species in old fields throws much light on the problems of succession.

The author wishes to thank Dr. Stanley A. Cain who suggested this problem and made many helpful criticisms.

## SUMMARY AND CONCLUSIONS

1. Old fields in the vicinity of Bloomington, Indiana, are often invaded by a certain assemblage of woody plants. Seven of the most important spe-. cies were studied. They were *Rhus copallina, Rosa setigera, Rubus alleghe-niensis, Populus grandidentata, Sassafras officinale, Symphoricarpos orbiculatus,* and *Smilax rotundifolia.*

2. These are better able to establish themselves than more mesophytic woodland plants and are important invaders because of the efficient means of vegetative propagation that all of them possess.

3. The roots of *Rhus copallina* fall into the specialized prominent lateral type. Shoots arise from the laterals, the average advance per year of the new shoots being 73 cm.

4. *Rosa setigera* was found to possess both roots of the prominent lateral type and of the generalized type.

5. The roots of *Rubus alleghenicnsis* consist of a large number of branching laterals, rhizomatous in habit, with numerous vertical roots attached to them. The roots penetrate to a depth of 103 cm. but were mostly above 80 cm.

6. The main lateral roots of aspen are seemingly devoted to reproduction. They are rarely deeper than 30 cm., the shoots developing from them when nearest the soil surface. The rate of spread averages 103 cm. per year.

7. Shoots arise from the lateral roots of sassafras at all depths. Shoots are found to invade new areas at the rate of 73 cm. per year.

8. *Symphoricarpos orbiculatus* reproduces vegetatively only by above-ground runners in southern Indiana. This is quite different from the reproduction by rhizomes as found by Weaver in eastern Nebraska.

9. *Smilax* propagates by means of shallow underground rhizomes which possess nodes with a scaly bract. They tend to radiate from a central mass of rhizomes from which most of the roots originate. Roots arise only from the nodes and rarely penetrate as deeply as 1.5 meters.

10. The origin of a new shoot in all species propagating from roots causes an enlargement of the root in the vicinity of the shoot and a development of additional feeding roots.

11. In all species the roots are very shallow, obtaining water and nutrients from the top layers of the soil.

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# TESTING RAUNKIAER'S LAW OF FREQUENCY AGAINST DISTRIBUTION OF FISHES IN THE STREAMS OF WAYNE COUNTY, INDIANA [1]

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As a part of a series of studies in the ecology and taxonomy of fishes of the streams of Wayne county in eastern Indiana, data were taken on the numbers and distribution of all the species of fishes recorded in the area. In the light of recent tests of plant and animal distribution against Raunkiaer's Law of Frequency, it appeared that these data might be used as a further test of the law and with respect to a hitherto unanalysed group of animals.

Raunkiaer's Law of Frequency states that in an association several species prosper at the expense of the rest, thus producing at one extreme a class with relatively few species but a great many individuals, and at the other extreme another class with a very small number of individuals representing rare and sporadic species.

Raunkiaer's work on plant distribution was written in Danish and has just become available to American biologists by a recent English translation (Raunkiaer, '34). However the principle has been tested by a number of American biologists. Raunkiaer divided species of plants into five classes depending on the frequency with which they occurred in sample areas. The sample areas or quadrats chosen by Raunkiaer were definitely measured, usually 0.1 sq. m. He classified his forms into five frequency classes as follows: A including those species occurring in 1–20 per cent of the sample areas; B in 21–40 per cent; C in 41–60 per cent; D in 61–80 per cent; and E in 81–100 per cent. He found that the classes were related to each other with respect to the number of species each contained by the following formula; $A > B > C \gtreqqless D < E$. A typical series of numbers taken from his work is 53; 14; 9; 8; 16.

Kenoyer ('27) stated that Raunkiaer's law " was found to hold good for distribution of insects in grassland and for microorganisms in hay infusion." He also pointed out that the letters on a printed page, taken at random, have the same kind distribution.

Hanson and Ball ('28) applied Raunkiaer's law to grazing studies. In order to study the effect of grazing on vegetation they located sample areas

on two types of pasture, deferred rotation pasture and continuously grazed pasture. They found that continuously grazed pasture differed from the deferred rotation types in that the plant species were more numerous in class D than in class E. They believed that they could determine the extent of overgrazing by the extent of deviation from Raunkiaer's normal curve.

Romell ('30) pointed out that the Raunkiaer principle is not restricted to homogeneous plant associations but applies to large areas with varied vegetation such as whole provinces or even islands. However, in order to be able to compare results he showed the necessity of agreeing upon sample areas of a standard size such as 0.1 sq. m. which was the area used by Raunkiaer.

Cain ('32) has given an excellent discussion of the concepts involved in the application of Raunkiaer's law including a good definition and discussion of the frequency classes.

McGinnies ('34) working with plant distribution in a semi-arid region called attention to the high degree of correlation between frequency index and abundance. He gave data showing a high degree of correlation between frequency indexes from quadrats of 0.1 sq. m. and 1 sq. m. showing that the size of the quadrat used had best be determined by the conditions encountered.

The work done in the present study was not primarily for the testing of Raunkiaer's Law of Frequency. The data represent the results of twenty-five collections from stations scattered throughout the county, an area some twenty miles square. The collections were taken between May and September, 1934. A total of forty-five species with 18,296 individuals was taken. The species, with respect to the number of stations where they occurred and the number of individuals taken are listed in table I.

The analysis of these data suggested the following problems: (a) whether the distribution, by species and by individuals, conforms to Raunkiaer's law; and (b) whether Raunkiaer's procedure of arranging species into frequency classes would be more useful in analyzing distribution than more subjective methods which describe occurrences as " abundant," " rare," etc.

Ordinary quarter inch mesh minnow seines varying in length from eight to thirty feet were used. Instead of attempting to standardize the seining methods, such as by using a certain number of sweeps, it was found more practicable to use whatever methods were adapted to that particular sample area in order to obtain representatives of all species occupying this area. Thus the collections were approximately equally efficient in the different habitats rather than being rigorously standardized by other criteria.

The dominant species are found in class E, where there is a much larger number of individuals than in any of the other classes. Two of these species *Notropis cornutus* and *Hyborhynchus notatus* occurred in all twenty-five of the sample areas. Table I shows a decreasingly wide range of distribution from the above species to two species *Entosphenus appendix* and *Pomoxis annularis* which were taken only as single individuals. It is to be noted that certain species notably the gizzard shad (*Dorosoma cepedianum*), the

TABLE I. *Species of fishes taken in twenty-five sample areas from streams of Wayne County Indiana*

| | Number and Per Cents of Sample Areas in Which Each Species was Found | | Total Number of Individuals |
|---|---|---|---|
| Notropis cornutus chrysocephalus (Rafinesque) | 25 | 100% | 3239 |
| Hyborhynchus notatus (Rafinesque) | 25 | 100% | 3069 |
| Campostoma anomalum (Rafinesque) | 24 | 96% | 1695 |
| Ericymba buccata Cope | 22 | 88% | 570 |
| Notropis lythrurus (Jordan) | 21 | 84% | 2195 |
| Semotilus atromaculatus atromaculatus (Mitchill) | 21 | 84% | 798 |
| Poecilichthys coeruleus (Storer) | 20 | 80% | 257 |
| Notropis deliciosus stramineus (Cope) | 17 | 68% | 1264 |
| Boleosoma nigrum nigrum (Rafinesque) | 17 | 68% | 201 |
| Micropterus dolomieu Lacépède | 16 | 64% | 231 |
| Hypentelium nigricans (Le Sueur) | 16 | 64% | 205 |
| Etheostoma blennioides blennioides (Rafinesque) | 16 | 64% | 128 . |
| Hybopsis amblops (Rafinesque) | 13 | 52% | 332 |
| Notropis photogenis (Cope) | 12 | 48% | 266 |
| Moxostoma erythrurum (Rafinesque) | 12 | 48% | 144 |
| Catostomus commersonnii commersonnii (Lacépède) | 12 | 48% | 110 |
| Notropis volucellus (Cope) | 11 | 44% | 204 |
| Ambloplites rupestris (Rafinesque) | 11 | 44% | 69 |
| Nocomis biguttatus (Kirtland) | 11 · | 44% | 68 |
| Xenotis megalotis megalotis (Rafinesque) | 11 | 44% | 41 |
| Notropis rubellus (Agassiz) | 10 | 40% | 808 |
| Poecilichthys spectabilis Agassiz | 10 | 40% | 111 |
| Hadropterus maculatus (Girard) | 9 | 36% | 60 |
| Rhinichthys atronasus (Mitchill) | 8 | 32% | 884 |
| Percina caprodes caprodes (Rafinesque) | 7 | 28% | 35 |
| Notropis whipplii spilopterus (Cope) | 6 | 24% | 264 |
| Pimephales promelas promelas Rafinesque | 6 | 24% | 42 |
| Nocomis micropogon (Cope) | 6 | 24% | 26 |
| Chrosomus erythrogaster Rafinesque | 5 | 20% | 203 |
| Cottus bairdii bairdii Girard | 5 | 20% | 147 |
| Moxostoma duquesnii (LeSueur) | 5 | 20% | 10 |
| Carpiodes cyprinus (Le Sueur) | 4 | 16% | 6 |
| Dorosoma cepedianum (Le Sueur) | 3 | 12% | 524 |
| Cyprinus carpio Linnaeus | 3 | 12% | 19 |
| Poecilichthys zonalis Cope | 3 | 12% | 11 |
| Apomotis cyanellus (Rafinesque) | 3 | 12% | 10 |
| Phenacobius mirabilis (Girard) | 3 | 12% | 10 |
| Catonotus flabellaris flabellaris (Rafinesque) | 3 | 12% | 8 |
| Ameiurus melas melas (Rafinesque) | 3 | 12% | 3 |
| Moxostoma anisurum Rafinesque | 2 | 8% | 16 |
| Ameiurus natalis (Le Sueur) | 2 | 8% | 7 |
| Aplites salmoides (Lacépède) | 2 | 8% | 2 |
| Helioperca incisor (Cuvier and Valenciennes) | 1 | 4% | 2 |
| Pomoxis annularis Rafinesque | 1 | 4% | 1 |
| Entosphenus appendix (De Kay) | 1 | 4% | 1 |
| | | | 18,296 |

red bellied dace (*Chrosomus erythrogaster*), and the black nosed dace (*Rhinichthys atronasus*), depart from this trend in that they were taken in large numbers in a few places. These forms are known to be limited to highly restricted habitats.

Due to the difficulty with which some species are captured, they were not taken in the proportion of sample areas in which they really occurred. Very young individuals went through the seine while very elusive ones as bass went around the ends or over the top. Carp were found to hide under logs and

roots along the banks while darters were difficult to take because of the habit of hiding between stones.    Mr. M. B. Trautman emphasized this problem in personal correspondence pointing out several instances in his own experience in which it was shown that ordinary seining methods did not obtain all species in their proper proportions.

Taking large numbers of small young at certain spawning seasons probably altered the uniformity of particular sample areas from the average studied throughout the season.    During a drought in August, streams which had been of average size earlier in the summer were little more than a trickle between pools.    Obviously this eliminated certain species and greatly concentrated certain others.    It was impracticable at the time of seining to confine the taking of specimens to a certain number of square feet of water surface, and it would be useless for the purpose of this paper to reduce the number of fishes taken in each sample area in proportion to the surface area or to the volume of water contained in them because it is the occurrence and not the number of specimens that is being dealt with.    These variables, with others possibly overlooked might mask the details of Raunkiaer's formula.

Raunkiaer's eleven groups of plant surveys referred to by Kenoyer ('27) gave a distribution in the frequency classes as follows: 53; 14; 9; 8; 16. Similar results were obtained by Kenoyer for insects, the frequency classes containing: 30; 3; 3; 0; 1.    A much closer correlation to Raunkiaer's formula was found by the same author for microorganisms in a hay infusion: 54; 9; 5; 5; 13.

The species as given in table I when arranged into five frequency classes according to Raunkiaer's method occur in the following numbers respectively 17; 8; 8; 6; 6.    Inspection of these numbers shows class E to be of the same size as class D instead of being larger as in the typical Raunkiaer distribution. Dr. D. H. Thompson has kindly aided in making a similar analysis of his own data (Thompson and Hunt, '30); in his case the number of species were represented in their respective classes as follows: 44; 10; 6; 3; 2.

The main significance of Raunkiaer's Law of Frequency as stated by Kenoyer ('27) and by Gleason ('29) is that there are more rare species than common ones.    In this light the results of this study were in accord with Raunkiaer's law.    It has been shown (Kenoyer, '27) that lack of uniformity in the area studied would account for departures from the usual situation, and that such departures might be made use of in analyzing the heterogeneity of the area.    It is known that the sample areas of the streams studied had different rates of flow, depths, kinds of bottom, etc.    It is possibly for this reason that the results obtained do not conform perfectly to the conventional distribution.    Dr. D. H. Thompson has pointed out in a personal communication that a normal distribution curve when plotted into five frequency classes, gives a distribution of numbers in the proportion of 58; 15; 13; 12; 22.    This was almost identical to the proportion of Raunkiaer's classes.    This, taken with the fact that inanimate things such as letters on a printed page have a

similar distribution, suggests material for fruther study of the basis of Raunkiaer's Law of Frequency.

## SUMMARY

1. The distribution of fishes in the streams of Wayne county shows a correlation with Raunkiaer's Law of Frequency similar to that of vegetation, insects, and microorganisms.

2. Difficulty of controlling size and uniformity of sample areas in streams renders Raunkiaer's methods of frequency analysis of less value for fishes than for plants.

3. Application of Raunkiaer's law is valuable in analysis of field records in that:

*a.* It reveals lack of uniformity in distribution which may lead to more detailed ecological study of the underlying factors.

*b.* It provides a more adequate method of measuring and evaluating frequency than does the use of subjective terms as " abundant," " rare," etc.

4. These results point out the urgent need for an improvement in the technique of taking representative samples of fishes.

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# AN AREA–LIST METHOD OF MEASURING RANGE PLANT POPULATIONS

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In the past, the Forest Service has used several different methods of measuring vegetation quantitatively in studying the relationship between herbaceous plant populations and range management (Forsling, '25). While these methods have provided data necessary for solution of the problems involved, they are limited in their application or else do not yield data sufficiently reliable for all purposes.

The most widely used of these methods involves an ocular estimate of the density and composition of the vegetation on natural range units or on small research plots. Whereas this method is useful for determining major plant relationships, its susceptibility to error due to misjudgment by inexperienced or poorly trained observers and the limited amount of specific data obtained, make it objectionable from a research standpoint. Mere knowledge of the amount and character of the vegetation, although invaluable in making up a grazing plan for administrative use, is insufficient for an understanding of the exact nature and the causes of changes in plant population.

The quadrat method is another widely used system for recording changes in the plant cover (Hill, '20; McGinnies, '30). This system is accurate and provides unlimited data, including a permanent record of the exact location and the size and shape of the basal cross-section of every perennial plant within a definite area. Nevertheless, it too has its shortcomings. Owing to the small size (usually 1 sq. m.) of each sample, it is necessary to establish four or more quadrats for any given condition in order to obtain a reliable record of the changes occurring under that condition. It is impossible generally to maintain a sufficient number of quadrats for each set of conditions involved because of the time required for charting. Hence quadrats are used chiefly to supplement more extensive methods of describing the vegetation.

A third method typified by the list-quadrat system in which the individuals of each species occurring within a plot are carefully counted, has been used to some extent (Hanson and Ball, '28). While the resultant data indicate the composition of the vegetation, it does not show the quantity of vegetation on the ground in terms of density or volume. In other words, the method is highly satisfactory for qualitative analysis, but is limited for quantitative measurement to the comparison of areas on which the plant composition is similar and composed largely of single stalked species. It is not applicable to grasses or other turf-forming plants. Because of these deficiencies, the

list-quadrat has not been used extensively in grazing experiments. Instead, its chief use has been in specialized research dealing with single species, such as stock-poisoning plants or plant indicators.

The area-list method as here described combines many of the advantages of each of the previously employed methods, and yet is free from their major disadvantages. However, it is not intended to replace but rather to supplement the older systems of measurements in obtaining an accurate and detailed description of range plant communities.

## DESCRIPTION OF THE METHOD

The area-list method was evolved in an intensive investigation of plant relationships to soil erosion on the watershed of the Boise River in southwestern Idaho. In this study it was necessary to determine the area and number of the individual plants on many sample plots, in addition to reliable density and composition data. As many quadrats were established as time would permit, but it was found necessary to supplement the chart quadrat system of measurements with larger plots on which reliable data could be obtained through less intensive examination.

The method developed for this purpose is based upon the determination, by actual measurement with an especially marked scale, of the area of the vertical projection of the foliage of each perennial plant on every plot or major quadrat under study. The foliage of each plant is compressed by hand to circular formation, through which the ground cannot be seen. The area of this clump is then read directly on the special scale, which is laid across or inserted through the compressed plant (fig. 1). The scale is graduated so as to show the area of circles of various diameters. Comparison of the scale with the metric rule, as shown in figure 2, discloses that a circle with a diameter of approximately 3½ centimeters for example, has an area of 10 square centimeters, one with a diameter of approximately 10 centimeters, an area of 80 square centimeters, etc. The figures of area used on the scale were chosen so as to provide an interval which increases as the diameters of the plants increase in order to keep the error in measurement at a nearly constant value, and also to provide numbers which could be conveniently handled in compilation. The intervals on the scale are small enough to measure the areas of plants as accurately as the nature of the subject will permit.

Because of their short life cycle, annual plants are not measured individually. Instead, the examiner estimates the total area of all the plants of a species by mentally massing them into a circle of unit density, and measuring the area of this circle with the scale.

The details of the method are presented in the following instructions for field measurements.

*a.* All perennial plants shall be compressed until the foliage makes up tentenths density. If the plant does not grow in a circular clump, it will be

FIG. 1.  The area scale being used to measure a plant of *Oryzopsis hymenoides* 30 square centimeters in area.

rounded off until the average diameter can be determined.  The area scale will then be laid across this diameter and the projection area of the plant thus obtained will be recorded.

*b.* Perennial plants, the centers of which have died, shall be given two measurements.  In addition to the projection area of the entire clump, the area of the dead portion shall be determined in the same manner.  This shall be entered on the form as being subtracted from the total area; *e.g.* 20–4, or in
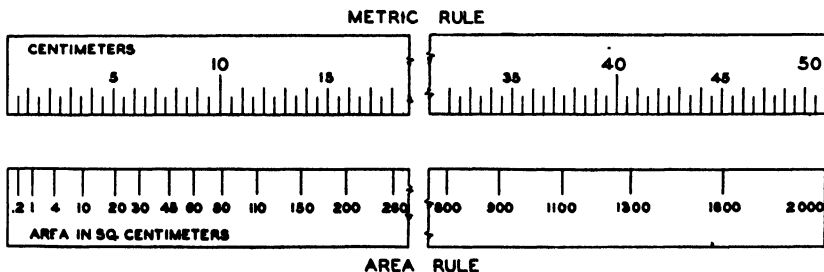


FIG. 2.  The area rule and an ordinary metric rule, showing the graduations on the special scale whereby areas of circles of different diameters can be measured.  For convenience the area rule may be marked on the back of a regular metric rule.

the case of a plant all of which has recently died, 20–20. In compilation, only the living portion of the plant will be considered as making up density.

c. Seedlings will not be measured, but counted. Before leaving the plot, the examiner will arrive at an average figure for the area of seedlings of each species, which will be used in determining the density of seedlings on the plot.

d. Annual species will not be measured individually, but the total area of ground covered by the species shall be estimated with the aid of the scale, and this figure recorded.

In practice, plots 5 by 5 meters are used. These plots are divided by tapes into strips 1 by 5 meters, the plants in each strip being measured and recorded separately. This division affords data on the distribution of species within the plot and insures against sacrifice of the entire plot if one to four of the strips are unduly damaged by unforeseen circumstances. The division is also helpful to the examiner, since a strip one meter wide is the most convenient for progress over the plot. The data are recorded on a special form on which the number of plants of each species is tallied by area classes with the ten point tally system (fig. 3). Records of the presence of and area covered by rodent mounds, fecal matter, alluvial deposits, stumps, logs, rocks and other noteworthy features of the plot are made on the same sheet. In addition, adequate supplemental notes concerning condition of the vegetation, slope, aspect, soil erosion, utilization by stock, and other biotic influences are made for each plot or area. The services of a second man, who need not be skilled or familiar with the flora, have been found valuable in making the records.

The compilation of the data is simple, rapid, and not readily subject to major errors. The area of each species is determined by totaling the area made up by each size class recorded. This is then converted into species density by expressing it as a decimal fraction of the total area of the plot. The total density of the plot is the sum of the individual species densities. An actual example of compilation of the data for one strip of a representative plot should make the compilation procedure clear.

In the example used (fig. 3), *Agropyron inerme* is considered first. Fifteen plants of this species having an area of 1 square centimeter each are recorded, giving a total of 15 square centimeters for plants of this area class. This figure is entered in the lower right-hand corner of the appropriate block on the form. There are 24 plants with an area of 4 square centimeters each, or a total of 96 square centimeters; 27 plants with an area of 10 square centimeters each, or a total of 270 square centimeters, and so on, for each of the size classes listed. In addition, the examiner found 5 plants, portions of which were dead, which were entered as follows: 400–260, 260–200, 200–150, 200–150 and 110–110. These have a living area of 140, 60, 50, 50 and 0 square centimeters, respectively. The total areas of each of the different size classes and the net living parts of the dead centered plants show the total area of *A. inerme* on the 1 by 5 meter strip to be 2,746 square centimeters. The total

Plot ...*FALL CREEK 4*...........................  Location.*EAST SIDE FALL CR ENCLOSURE*...
Strip No...*2*.................................  Time Required to Map Plot..*1 HOUR*..........
Total Density..*179*.........................  Date...*AUGUST 29, 1931*......................
Examiner: *C.K.R*     Recorder: *E.R.C.*

| Species | AGROPYRON INERME | MELICA BELLA | BROMUS MARGINATUS | | LUPINUS COMATUS | LAPPULA DIFFUSA | |
|---|---|---|---|---|---|---|---|
| Density | .055 | .011 | .006 | | .105 | .002 | |
| Seedling | | | | | AREA = 2 ⊠⌐ = 32 | | |
| .2 | | | | | | | .2 |
| 1 | ⊠ ‒ ·· 15 | ⊠ ‒ ·· 16 | ⊠ ⊠ ⊠ 30 | | | | 1 |
| 4 | ⊠ ·· · ⊠ 96 | ⊠ ☐ 72 | ⊠ ·· ⊠ 92 | | ⌐ ·· | 20 | 4 |
| 10 | ⊠ ⊠ ⊏ 270 | ⊠ ·· 140 | ⊠ ·· 130 | | ◨ 90 | | 10 |
| 20 | ⊠ ⊠· · 460 | · · 60 | · · 60 | | ⊠ · 240 | | 20 |
| 30 | ⊠ 300 | · · 60 | | | ⊠ ⊠ 600 | | 30 |
| 45 | ·· 135 | · 45 | | | ⊠ · 435 | | 45 |
| 60 | ·· 120 | · 60 | | | ⊠ 480 | | 60 |
| 80 | ·· 160 | · 80 | | | ⊠ ·· 960 | | 80 |
| 110 | ·· 220 | | | | ·· 330 | | 110 |
| 150 | · 150 | | | | ·· 300 | | 150 |
| 200 | · 200 | | | | · 200 | | 200 |
| 260 | · | | | | | | 260 |
| 320 | · 320 | | | | · 320 | | 320 |
| 400 | | | | | | | 400 |
| 500 | | | | | · 500 | | 500 |
| 600 | | | | | | | 600 |
| 700 | | | | | · 700 | | 700 |
| 800 | | | | | | | 800 |
| 900 | | | | | | | 900 |
| 1100 | | | | | | | 1100 |
| 1300 | | | | | | | 1300 |
| In addition | 400 -260 140 260 -200 60 200 -150 50 200 -150 50 110 -110 — | 150 -110 40 | | | | | In addition |
| Total | 2746 | 572 | 312 | | 5267 | 100 | |
| Density | .005 | .011 | .006 | | .105 | .002 | |

Fig. 3. The field form used for recording plot data by the area-list method, showing the character of data obtained.

areas for the other species are determined in the same manner and in the example used are; 572 square centimeters of *Melica bella*, 312 square centimeters of *Bromus marginatus,* and 5,277 square centimeters of *Lupinus comatus. Lappula diffusa* being an annual species is not measured by individuals, but the total area of the species was estimated and recorded as 100 square centimeters.

These areas are expressed next in terms of decimal fractions of the total area of the strip. Each strip of 1 by 5 meters has an area of 50,000 square centimeters, and since 1 square centimeter is .00002 of this amount, it is necessary to multiply the species area by this factor to obtain the density figure for the species. Upon application of this factor, the density of *A. inerme* is found to be 2,746 times 0.00002 or 0.055; that of *M. bella*, 0.011; of *B. marginatus* 0.006; of *L. comatus* 0.105; and of *L. diffusa* 0.002. The total density for the strip is the sum of all these species densities or 0.179. The average density of each species for the 5 by 5 meter plot is determined by averaging the species density of 5 strips. The sum of the average species density gives the total density for the plot.

An example of how the data may be interpreted is presented in figure 3. These data indicate that about 18 per cent of the strip surface is covered with vegetation. *A. inerme* alone covers 5.5 per cent of the available ground surface, *M. bella* 1.1 per cent, *B. marginatus* 0.6 per cent. Thus, both the absolute and the relative amount of the cover provided by each species is readily determined. Furthermore, most of the plants of *A. inerme* on this strip have an area of 10 to 20 square centimeters, with no plants of this species larger than 320 square centimeters in area whose centers have not died, while no seedlings of *A. inerme* were present. Similar data for each of the species listed are given. If a change in density is shown by measurements in subsequent years, it will be possible to trace this to (1) growth (or decadence and death) of all or of certain size classes of plants established at the time of the first record, or (2) establishment of new individuals. Thus, the cause of change in plant density can be easily ascertained.

The area-list method has been found to be very satisfactory after five seasons' use on the Boise River watershed. It is more accurate than all other methods in use except the chart quadrat method, due mainly to the use of the scale as a measuring stick, which greatly decreases the need for judgment and reduces the tendency of personal error, and because the examiner must go over the entire plot in a systematic manner, examining every square inch of the ground. It requires less time for measurement and compilation than the charting and compilation of an equally good sample of vegetation by the quadrat method, only about 1¼ hours being needed for the field work on each plot. Moreover, larger and more representative samples of vegetation can be measured than is practicable by the quadrat method and the data obtained are in sufficient detail for research purposes. For example, it provides data not only regarding the density of the species but also regarding the number of plants of each species by size classes.

The method has been found to be most useful for the study of clump-forming species, such as *Agropyron inerme*, *Stipa lettermanii*, *Balsamorhiza sagittata*, *Astragalus spp.* and *Lupinus spp.* The method may not be as applicable to vegetation growing in dense stands or composed largely of single stalked species. Its general usefulness may be extended, however, by

modifying it slightly to suit specific conditions. It may be adapted to denser stands of vegetation by reducing the size of the plot; or it may be applied to areas as small as 1 square meter, as an intermediary between the list quadrat and the chart quadrat. The method seemingly would be especially valuable in belt transect studies, where, because of the heterogeneous character of the vegetation, it is often difficult to obtain satisfactory ocular estimates or other description. The success of the method where used fully warrants trial under other conditions of vegetation and on different types of plots in other localities.

## SUMMARY

A new area-list method of describing and quantitatively measuring herbaceous range plant populations and their changes is presented. The method is based upon the measurement, by the aid of a special scale, of the vertical projection foilage area of every plant growing within the plot. The measurements are tabulated by species on an appropriate record, facilitating calculation of the total projection area and the density for every species. Accurate data are thus provided concerning: (1) The total density; (2) the species density (composition); (3) the number of plants of each species present; and (4) the size of each plant growing on the plot. Although subject to certain limitations and not entirely free from the possibility of personal error, the method is considered an improvement in that it provides more reliable data than several of the previously described methods and is less laborious than the more reliable quadrat method. This new method would appear to be applicable, with slight modification, to a wide variety of field conditions.

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# AVAILABLE NITROGEN AS A FACTOR INFLUENCING THE OCCURRENCE OF SITKA SPRUCE AND WESTERN HEMLOCK SEEDLINGS IN THE FORESTS OF SOUTHEASTERN ALASKA [1]

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The region known as Southeastern Alaska lies in the northwestern part of North America between latitudes 54° and 60° N. and longitudes 130° and 138° W. It bounds northern British Columbia on the west, extending from the peaks of the coast range over a belt of mainland and myriads of islands to the open Pacific.

The central part of the coast range throughout its length is composed of an immense core of granite and diorite, which is evident also in the central portion of the larger mountainous islands. Bands of metamorphosed strata, often folded, and in places several miles in width, border this core and are in turn bordered at lower elevations by beds of sandstones, shales, limestones, volcanic lavas and tuffs.

The climate is moderate with heavy precipitation (table I) well distributed throughout the year; this results in a dense forest growth which covers the mainland and islands from sea-level to approximately 1500 feet elevation. The entire panhandle of Southeastern Alaska, with insignificant exceptions, is included within the Tongass National Forest.

The fact that the region under consideration is geologically young partially explains the shallowness of the soils. An extensive survey by the U. S. Forest Service in Southeastern Alaska indicates that less than one-tenth of one per cent of the area may be classed as potential agricultural land. Areas of possible agricultural value are generally small alluvial deposits located at the mouths of streams.

In general the soils supporting commercial forest stands may be classified as to parent material either as mainland soils developed from igneous rocks, granites and diorites, or the lower slope soils of the islands which commonly have been derived from limestones. The recently formed glacial moraines have been derived from igneous rocks and usually do not support commercial timber, the lack of large trees on such areas being chiefly due to their extreme youthfulness. Because of the relatively deep character of the soil material glacial moraines are potentially good forest sites. As the soil body develops under the influence of climate and the pioneer vegetation, a

TABLE I.   *Temperature and rainfall data Southeastern Alaska* [1]

| Month | Juneau | | | | Ketchikan | | | |
|---|---|---|---|---|---|---|---|---|
| | Max. temp. | Min. temp. | Aver. temp. | Precipi- tation | Max. temp. | Min. temp. | Aver. temp. | Precipi- tation |
| January | | | 27.7 | 7.16 | | | 32.1 | 14.04 |
| February | | | 30.2 | 5.59 | | | 34.6 | 12.51 |
| March | | | 33.7 | 5.51 | | | 37.2 | 12.88 |
| April | | | 40.5 | 5.31 | | | 41.7 | 11.66 |
| May | 55.6 | 40.0 | 47.7 | 5.25 | 55.7 | 39.0 | 50.3 | 8.40 |
| June | 62.9 | 46.0 | 54.2 | 3.76 | 62.9 | 45.4 | 54.2 | 6.01 |
| July | 64.2 | 49.9 | 57.0 | 4.91 | 65.4 | 49.2 | 57.4 | 8.41 |
| August | 61.7 | 49.3 | 55.3 | 7.18 | 66.0 | 50.3 | 58.1 | 12.28 |
| September | 56.1 | 44.2 | 50.2 | 10.43 | 61.6 | 45.2 | 53.1 | 12.45 |
| October | | | 43.2 | 10.94 | | | 46.0 | 21.13 |
| November | | | 35.3 | 8.50 | | | 39.1 | 20.38 |
| December | | | 31.1 | 7.59 | | | 36.2 | 16.73 |
| Yearly average | | | 42.2 | 82.13 | | | 45.0 | 156.88 |

[1] Data from U. S. Weather Bureau, Juneau, Alaska. Basis Ketchikan, 22 years; Juneau, 37 years. Temperature in degrees Fahrenheit and precipitation in inches.

humus layer forms which may be termed a thin mull. This humus type which is characteristic of the early successional stages on glacial moraines appears to be more favorable for forest growth than are the types which prevail under climax stands.

No systematic attempt has been made to apply the humus type classification of Romell and Heiberg ('31) in Southeastern Alaska. On the basis of general observation it seems probable that fibrous duff is the most common type of humus layer. Podsolized soils with leached layers up to fifteen or twenty centimeters in thickness are common. The most unfavorable duff types are found under dense hemlock stands. The mull types of humus layer occur only occasionally, being generally confined to areas supporting a growth of alder, or relatively open spots of elder bushes and grass. It seems reasonable to expect that on the cut-over areas some of the more favorable duff types may change to mull types under the influence of exposure and development of hardwood shrubs.

In order to furnish a background for the investigation here reported it seems desirable to outline the general conditions existing within the forests of Southeastern Alaska. There is included within the Tongass National Forest an immense area, roughly sixteen million acres. Heintzleman ('28) estimates that approximately 3 million acres of National Forest land in this region support 80 billion feet, board measure (hereafter abbreviated b.m.), of commercial timber. Of this total volume western hemlock, *Tsuga heterophylla*,[2] comprises approximately 74 per cent; Sitka spruce, *Picea sitchensis*,

[2] Excepting in those cases where the authority is stated the nomenclature of Sudworth ('27) is followed for the trees; that of Henry ('15) is followed for the lesser vegetation.

20 per cent; western red cedar, *Thuja plicata,* 3 per cent; and Alaska cedar, *Chamaecyparis nootkatensis,* 3 per cent.

Although the forest is a mixture of the two principal species, hemlock and spruce, pure stands of each occur locally. Studies by the writer ('32) indicate that the present old growth represents the climatic climax of the region, and that pure stands of spruce represent a less advanced stage of succession. Pure spruce stands develop as primary successions on recently formed glacial moraine plains.

In 1924 a general survey was made to determine the progress of re-stocking on cut-over areas of Southeastern Alaska, and since that time certain cuttings have been periodically examined in order to follow the trend of restocking and vegetative change. Most areas were found to be adequately restocked 10 years after cutting, and as forest fires seldom occur, due to the rainy climate, the regeneration is permanent.

However, the relative amounts of spruce and hemlock in the regeneration are subject to wide variations. Parts of certain areas reproduced heavily to spruce, while others showed a predominance of hemlock. Exposed mineral soil, and soil mixed with debris and piled up on the lower slopes by slides, old Indian garden sites long since abandoned, and recently uncovered glacial out-wash were found particularly favorable to spruce regeneration. On the other hand, the forest floor under old stands, especially on the many moss-covered logs and areas of decaying wood, seemed unfavorable for spruce. Hemlock, however, did well on such acid, peaty seedbeds; it appeared frequently on muskegs and formed stunted thickets on the poorer soils.

This variation in composition is significant not only because of the pulp and timber values involved (spruce being more valuable than hemlock) but also because of the silvicultural effects of the association of the two species. Recently completed studies by the Forest Service (Taylor, '34) demonstrate that natural pruning and height growth are poor in second-growth stands of pure spruce. Extremely slow growing thickets result when hemlock develops with but little spruce in mixture. Mixed stands of spruce and hemlock have higher yields than pure stands of either species; the hemlock forming a large part of the understory, thus favoring better natural pruning and increased growth of spruce.

In view of the importance of obtaining a sufficient amount of spruce in second-growth stands on cut-over areas, a study of factors affecting its regeneration and development was contemplated. A comprehensive study of all factors should be made and it was necessary to begin with the most significant.

The outstanding work of Hesselman ('17, '26, '27) with raw-humus soils and the investigations of others have clearly demonstrated the importance of available nitrogen for vigorous seedling development. Extensive field observations by the writer in Southeastern Alaska indicated that spruce seedlings occurred in greatest abundance on seedbed types in which active nitri-

fication might be expected; hemlock seedlings occurred more commonly on seedbed types in which less active nitrification would be expected. Consequently it seemed desirable to determine the influence of ammoniacal and nitrate nitrogen upon the occurrence of seedlings of the two species.

The purpose of the investigation as finally undertaken was: (1) to determine whether nitrogen in the form of nitrates or ammonia was a factor of importance in influencing the occurrence of Sitka spruce or western hemlock seedlings, (2) to study the nitrifying capacity of the more common seedbed types of cut-over land or glacial outwash. The investigation was pursued along the lines of field sampling, in which 500 meter-square plots were examined and soil samples taken, and periodic testing of soils in pot cultures for nitrate and ammoniacal nitrogen.

## Review of Literature

There appears to be little in forestry literature bearing directly upon the relation of soil nitrogen to the reproduction of trees, but many investigators have touched upon the importance of the formation of nitrates and ammonia during decomposition of forest humus. There is even less information on the relative importance of nitrogen in available form for individual species.

Müller (1887) was apparently the first to study forest soils in relation to tree growth. He distinguished two broad types of soil, namely mull and " torf " or " mor," later called respectively " brown earth " and " raw humus " by Ramann (1890). Müller pointed out the typical horizons appearing in a soil having torf as a humus layer and mentioned its unfavorable effect on young trees. This effect has since been noted by others, notably by Hesselman ('17, '26, '27).

The common brown earth type, according to Tamm ('30a), has a mull covering 0.5 to 25 cm. thick and beneath it a brown layer 30 to 100 cm. The torf, or raw-humus type (Tamm, '30b) are podsolized soils, characterized by a layer of raw humus 4 to 6 cm. thick and a bleached layer 10 to 12 cm. thick. Vaccinium-rich coniferous stands with sphagnum moss are typical of the latter. Romell and Heiberg ('31) in classifying the humus layers of forest soils retain Müller's term " mull," but change his " mor " to the American term " duff." Each is then subdivided into four types, all of which undoubtedly occur in Southeastern Alaska. The duff types, however, are more common than the mull types.

Müller, according to Melin ('25), drew attention to the poor development of spruce in the heath plantations of Westjutland and stated that the poor growth was corrected by interplanting with mountain pine, which fact he ascribed to an ability of *Pinus montana* Miller, to fix atmospheric nitrogen by means of its " forked mycorrhizae." This latter assumption was controverted by Möller ('06), who concluded after experimentation that *Pinus montana* could not assimilate atmospheric nitrogen. Gainey ('17) noted that

ammonia accumulated in the soil at times when nitrification was impossible and Hesselman ('17) considered the absence of regeneration or the poor growth of seedlings on heaths due to a lack of nitrification of ammoniacal nitrogen.   Hesselman later ('26) found that the mobilization of nitrate nitrogen was of the greatest importance for pine and spruce reproduction in northern Sweden.   Elaborating on the results of these experiments Hesselman ('27) grew pine and spruce under controlled conditions and showed that some of the most unfavorable raw humus types will react to the altered conditions following clear cutting and form nitrates, with remarkable improvement in growth of reproduction.   In the section of the present paper dealing with pot cultures, the writer will show that similar results may be expected in Southeastern Alaska.                                                    •

Hicock and associates ('31) found no consistent relationship between site index and the transformation of nitrogen to available forms in plantations of red pine, *Pinus resinosa*, in Connecticut.   They concluded that stands of the age classes included in the investigation (evidently 12–25 years) are able to obtain adequate amounts of nitrogen for the maintenance of a favorable rate of growth.   In most cases very little nitrate nitrogen was produced and ammonia was thought to be the chief source of nitrogen in the nutrition of these comparatively young red pine stands.   In the section on pot cultures it will be shown that several seedbed types from dense stands of timber produced almost no nitrate nitrogen during incubation.   Ammonia, but little nitrate nitrogen, was formed in two of the most common types; therefore it would seem that ammonia may be the chief source of nitrogen in the closed stands of Southeastern Alaska.

Tiedjens and Blake ('32), working with apple trees, noted that they absorbed ammoniacal nitrogen without oxidation to the nitrate form.   In soils of comparatively low pH values ammonia was apparently oxidized to the nitrate form before assimilation occurred.   If the pH of the soil was sufficiently high, ammonia was apparently assimilated directly without oxidation to the nitrate form.

That many other factors affect the growth of seedlings on raw humus was demonstrated by Moore ('26) and by Barr ('30).   Moore grew seedlings on raw humus in northern New England and found that even if the seed germinated the roots could not penetrate the dry duff.   Barr found the condition of the forest floor in spruce-fir forests of British Columbia unsuitable for the establishment of spruce seedlings, even after cutting and a period of " ripening " of the humus layers.   Westveld ('31) showed that advance reproduction in spruce stands must be established in the pulp-wood forests of the Northeast before the mature forest is cut off.   Barr was working with *Picea engelmannii* and *Picea glauca*, two species of comparatively dry, cold regions; Westveld and Moore with *Picea rubra*.   The climatic conditions prevailing over the range of these three spruces are not comparable to those of Southeastern Alaska.   Westveld mentioned that decayed logs are

frequently covered with dense masses of spruce and fir reproduction which in vigor and abundance exceed the reproduction on adjacent soil areas of equal size, indicating that decayed logs are most favorable to the germination and development of spruce and fir seedlings.    The wet, acid pulp of decaying logs in Southeastern Alaska is later shown to be a most unfavorable seedbed for Sitka spruce.

Romell and Heiberg ('31) showed that fibrous duff (very raw humus), which usually failed to show any nitrification after storage, did nitrify after considerable exposure following a clear cutting.    This development has also been observed by the writer and is discussed in a later section.    In investigating the various types of humus, Romell and Heiberg found that the duff types were mostly highly acid; nevertheless samples of pH 2.9 (probably the lowest value of humus layers on record) showed some nitrate formation. A positive correlation was found between pH and nitrification.

Aaltonen ('26) reported an increase in ammoniacal nitrogen with an increase in soil acidity, and an increase in nitrate nitrogen with a decrease in acidity.    The nitrogen in one form or the other varied from 0–350 p.p.m.[3] (air-dried soil).    Clarke ('24), working on the relation of soil acidity to the production of nitrates and ammonia, found that nitrates were present in measurable quantities in very acid soils, but since ammonia was greatest in these acid soils, he was of the opinion that nitrate production was affected somewhat by acidity.    This influence of acidity on nitrification was investigated by Hall, Miller and Gemingham ('08), who found that nitrification proceeded slowly despite the acidity of the soil.    Lunt ('32) showed that a positive correlation exists between nitrogen transformation and soil reaction. No definite relationship was found by the writer.

Migula ('00) was of the opinion that acid peat and certain acid forest soils do not contain the organisms necessary to induce nitrification, and Coville, according to Rigg ('16), held the same view.    Waksman ('27), however, stated that all soils except those that are extremely acid (below pH 4.0) contain bacteria capable of oxidizing ammonium salts to nitrites and the latter to nitrates.

Melin ('27) found that seedlings of pine and spruce growing on raw-humus soils develop best only when the nitrogen is made available by mycorhizas on their roots.    Two years previously he had demonstrated that tree seedlings cannot utilize atmospheric nitrogen (Melin, '25) and that the proper symbionts for each species may not be available in all localities.

McArdle ('32) showed that nitrogen is readily assimilated by seedlings without mycorhizas if the nitrogen is present in the form of inorganic compounds, but when this element is present only in organic compounds, especially complex proteins, the seedlings exhibit signs of nitrogen starvation.    In McArdle's cultures the presence of mycorhizas did nothing to alleviate this ap-

[3] Parts per million, abbreviated p.p.m.

parent starvation. Indeed, no conclusive proof was obtained to show that the presence of mycorhizas on the roots of seedlings was either beneficial or harmful.'

Nemec and Kvapil ('27) investigating the influence of forest stands on soil nitrate content and formation, found the uppermost soil layers richest in nitrates. This observation agrees with the findings of Waksman ('16) and others that the largest bacterial numbers are in the uppermost soil layers. According to Nemec and Kvapil the humus layers of heavy coniferous stands with no lesser vegetation had a tendency to denitrify. Less acid humus with moss did not denitrify, but formed no nitrates. Coniferous humus supporting a luxuriant growth of shrubs and herbs, even when highly acid, showed good possibilities of nitrification. Nemec and Kvapil found, as did Hesselman ('17), that nitrification increases and nitrophilous vegetation appears after cutting spruce stands. In mixed stands of conifers and broad-leaved species organic layers were found to be stronger in nitrifying power than those of pure stands.

Kvapil ('26) pointed out the favorable effect of mixed stands on growth. He found the nutrient content of the soil under pure beech stands to be higher than under pure spruce and equal to that under mixed spruce and beech. More available nitrogen was found in the mixed forest than in the pure spruce stand. Nemec and Kvapil ('25) demonstrated that less acid conditions obtain under mixed than under pure stands.

Hesselman ('26) showed that the humus produced by decaying birch leaves was capable of producing stronger and more vigorous plants than humus from pure spruce stands. He stated that birch, aspen, alder, willow, mountain ash, oak and beech influenced a change in an alkaline direction and that an admixture of hardwoods with conifers had a beneficial effect on growth.

One year old seedlings appear to show little reaction to an increase in available nitrogen. Palmer and Palmer ('30) found that applications of concentrated fertilizers such as Nitrophoska and urea to conifer seedlings resulted in doubling the growth of second year seedlings, but only a very slight increase in growth was noted in first year seedlings. In this investigation seedlings grown in pot cultures during one growing season showed no relationship to their seedbed type, probably for the same reason.

## METHODS

This investigation is based on simple field methods applied to a large number of samples, as contrasted to exhaustive laboratory technique applied to a smaller number of selected samples. The classification and analysis of a large number of plots tends to expose characteristics not always discoverable in applying intensive tests to a lesser number.

In the section on sample quadrats, the soil is called seedbed material, as

the manner of its collection precluded a more specific designation. In the section on pot cultures, the soils are classified, using the Romell and Heiberg terminology, as mull or duff, and further identified by the key plant on the plot, as hemlock-vaccinium duff, or sambucus mull.

## Sample Quadrats

As Lunt ('32) states, nitrogen transformation in the organic material of forest soils is dependent upon the properties of the material itself rather than upon the type of profile with which it is associated. Accordingly, meter square quadrats were examined on logged-off land without regard to profile type, trusting in a large number of samples to include all the common seedbed types. As the quantity of reproduction on given tracts was of no importance to the study, the plots were not taken at regular intervals along compass lines but were placed in selected beds of reproduction. Approximately half of the total number of plots were obtained on the southern part and half on the northern part of the Tongass National Forest.

The beds of reproduction were selected with a view to obtaining a wide range in percentage of spruce and hemlock seedlings extending from 100 per cent of spruce to 100 per cent of hemlock. In sampling, a wooden frame one meter square was placed on the area to be examined. Notes were taken of the number of spruce seedlings, the number of hemlock seedlings, the vegetation other than tree seedlings and the species which appeared to be the key plants on the plot. In selecting these the abundance alone was not the criterion. A small salmonberry bush, *Rubus spectabilis*, might have affected the character of the seedbed more than several times as many individuals of *Cornus canadensis*. The area influenced by the plant was considered of more importance than the number of individuals.

As newly germinated seedlings are not wholly dependent upon the soil for nourishment but gain part at least from the seed, the plots included only seedlings having attained a woody stem. On the other hand, no plots were taken in beds of seedlings whose roots had penetrated beyond the first three or four inches of soil; in this way fairly homogeneous samples were obtained. The tree seedlings ranged from one to 4 years of age.

## Treatment of Soils

Composite soil samples collected from around the roots of the seedlings on each plot were placed in muslin bags and taken to the drying racks where they were emptied on cheesecloth stretchers and air-dried. The samples were then stored in heavy paper bags to await transportation to the laboratory.

According to Lunt ('32) previous drying of the soil makes little or no difference in the amount of nitrogen transformed in a 3 months period of incubation.

## *pH Tests*

Soil acidity tests were made before incubation with the quinhydrone electrode, using a Youden electrometric set. No tests followed incubation as only field acidity was wanted. The soils were not ground or screened. As 500 samples were tested, bridges were replaced each day and new quinhydrone test solutions made every 2 hours.

## *Nitrate Nitrogen Tests*

Each soil sample was tested for nitrate nitrogen before and after a 3 months period of incubation. The microchemical soil tests developed by Morgan ('32) were used for both nitrate and ammoniacal nitrogen, the procedure being simple and sufficiently accurate for the purpose of this investigation. The relative accuracy of this method has been indicated by Morgan ('30).

The soil was placed in the Morgan test block and a few drops of distilled water leached through it. Clear leachate was obtained from muddy soils by drawing the discolored mixture into a medicine dropper, then carefully squeezing off one drop. Four drops of the test solution (0.05 gram diphenol-amine in 25 cubic centimeters of concentrated sulphuric acid) added to one drop of the leachate produced a blue color in the presence of nitrates. Comparison with a color chart indicated the quantity of nitrates in p.p.m. The test solution was renewed every 48 hours.

## *Ammoniacal Nitrogen Tests*

The test for ammoniacal nitrogen was similar in character. The extracting liquid was prepared by dissolving 25 grams of C. P. potassium chloride in 100 cubic centimeters of distilled water. One drop of Nessler's reagent added to 4 drops of the leachate produced an orange color in the presence of ammoniacal nitrogen. Comparison with a color chart indicated the quantity in p.p.m.

## *Incubation*

The soils were incubated according to Hesselman's method, mixing one-third humus material with two-thirds pure sand by volume. Distilled water was added until the mixture appeared to have optimum moisture content, after which it was placed in a numbered sample bottle, the top screwed on about halfway and stored at 70° F. In this manner sufficient air was allowed to enter for nitrate formation, yet not enough to seriously alter moisture conditions. Frequent determinations of water loss of the entire series being impossible, ten samples were weighed at 14-day intervals and the loss in weight averaged. An amount of distilled water equal in weight to the average loss of the ten samples was added to each bottle. Variation in moisture loss was small.

At the end of 3 months incubation, ammoniacal and nitrate nitrogen tests were made. Many soils would lose ammoniacal nitrogen through transformation to nitrates during incubation; others, not nitrifying, would increase their ammonia content. Tests for this form of nitrogen were not made before incubation as inconsistent results would be obtained.

## Computations

The field sheets were grouped according to information desired and the results tabulated. In the computations the percentage of hemlock is seldom mentioned, the spruce percentage being most significant. The spruce percentage divisions were from 0–9.9, 10–19.9, 20–29.9 per cent, etc. In sorting into nitrate nitrogen or ammoniacal nitrogen classes the plot sheets were grouped into divisions of 10 p.p.m. in a similar manner.

## Pot Cultures

Samples of each of the 10 more important and characteristic seedbed types were selected for study. These were:

1. Alder mull from glacial moraine.
2. Willow-poplar mull from glacial moraine.
3. Hemlock-Vaccinium duff from climax forest.
4. Rotten wood from dense hemlock stand, second growth.
5. Spruce duff from dense stand, second growth.
6. Hemlock duff from dense stand, second growth.
7. Sambucus mull from *Sambucus racemosa* thicket, cut-over land.
8. *Rubus spectabilis* mull from thicket, cut-over land.
9. Fatsia mull from *Fatsia horrida* thicket, cut-over land.
10. Alder mull from *Alnus sinuata* thicket, cut-over land.

*First Series.* These samples were mixed with pure sand in the proportions of one-third seedbed material to two-thirds pure sand, by volume, and set up in pots, a set of 3 being used for each type. One pot was planted with newly germinated spruce seedlings, another with similar hemlock seedlings, while the third was used as a check. In December, 1931, these were placed in a room kept at approximately 50° F.

At fourteen-day intervals, at a stated hour, the soil in each check pot was tested for nitrate nitrogen and an average of 2 results recorded until April, 1932, when the pots were transferred to the open. Tests were then made at intervals of seven days until the close of the experiment. The contents of the pots were moistened with pure water of neutral reaction, were kept at a constant optimum moisture condition determined by observation only, and were open to the air and sunshine. During periods of rainfall, the pots were covered by a canvas stretched over the series.

On October 11, 1932, the weekly tests were discontinued and the check

pots placed in a warm room to incubate for ten days, after which tests were made for nitrate and ammoniacal nitrogen.

*Second Series.* The results of the first series of nitrate nitrogen tests were erratic. In the hope of more consistent results a new series of tests was run using those seedbed types which in the first series had shown the greatest differences in nitrification, namely glacial alder mull, spruce duff, hemlock duff, *Rubus spectabilis* mull and alder mull. These were set up in the same manner as the pots in the first series but no seedlings were grown. The pots were placed in a room where the temperature, according to a thermograph record, did not vary from 72° F. by more than 2 degrees during the period of the tests.

Nitrate and ammoniacal nitrogen tests were made in triplicate daily, at a set hour, for 30 days and an average figure recorded for the 3 pots of each seedbed type. In addition sets of 3 small samples for each type were incubated for 2 months and at the end of that period tested for nitrate and ammoniacal nitrogen.

In the tests of the second series a more rapid and accurate technique developed at the Connecticut Agricultural Experiment Station was used, the soil sample being placed in a filter paper and a leaching solution used which allowed simultaneous testing for both nitrates and ammonia.[4]

## Results of the Investigation

### Relation of Spruce Percentage to Nitrate Nitrogen

The soil samples were tested both before and after incubation. The early tests showed no significant relationship but after storage the nitrate nitrogen was found to be an important factor in the occurrence of spruce seedlings.

Tests before storage were made principally to determine the gain in nitrates during incubation; the initial content in p.p.m., however, was so small the soils may be considered to have had no nitrate nitrogen before incubation. This is understandable, as the quantity in the air-dried samples would be equivalent to the amount not utilized by the vegetation at the time of collection. The plots being well covered with growing plants when the samples were collected, nitrate nitrogen was undoubtedly utilized as fast as it became available. The values obtained after storage indicate the approximate quantities available during the growing season.

The results of the final tests are presented in figure 1, which illustrates the relationship of nitrate nitrogen to the percentage of spruce. The range in quantity of nitrate nitrogen in each spruce percentage class is shown; for example, from 0 to 120 p.p.m. in the 0–9.9 spruce percentage class. The number of plots (frequency of occurrence) in each nitrate nitrogen class is also shown; 26 having a zero value, 5 having 5 p.p.m., 3 having 10 p.p.m., etc., in this spruce percentage class. The average value in p.p.m. of nitrate nitro-

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4 Personal correspondence.

gen for each spruce percentage class is shown by the connecting line which depicts a curve of relationship.

A slight increase in the percentage of spruce is noted as the nitrate nitrogen changes from 0 to 20 p.p.m., this increase becoming more definite as the
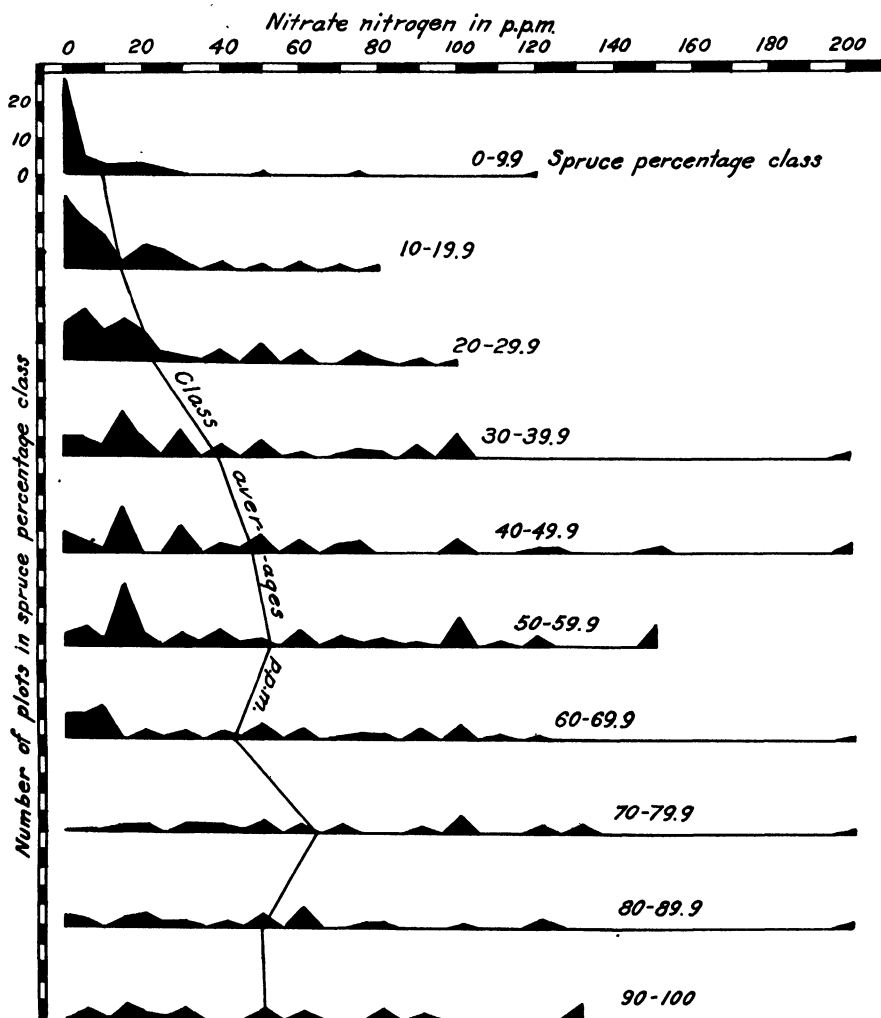


Fig. 1. Relation between soil nitrate nitrogen and spruce percentage. The distribution of plots with reference to nitrate nitrogen indicated for each of 10 spruce percentage classes.

quantity of nitrates rises to approximately 50 p.p.m. Any additional nitrate nitrogen in the soil beyond this point is of no significance. This type of curve is often termed by chemists a " saturation curve."

As illustrated in the relationship now being discussed, small quantities of nitrate nitrogen have little or no effect upon the percentage of spruce; slightly larger quantities react very strongly upon the percentage, but when a certain maximum is reached, additional amounts of nitrates are not accompanied by higher percentages of spruce. The amount of nitrates (50 p.p.m.) indicated at the point where the curve starts to level off is the approximate minimum requirement for a large percentage of spruce. It marks the saturation point, beyond which nitrates cease to be of importance in controlling the percentage of spruce.

In order to further illustrate the relationship of nitrate nitrogen to amount of spruce the percentage of plots within each spruce percentage class having zero p.p.m. and those having 50 or more p.p.m. of nitrate nitrogen were determined. These were plotted as shown in figure 2. Approximately 60 per
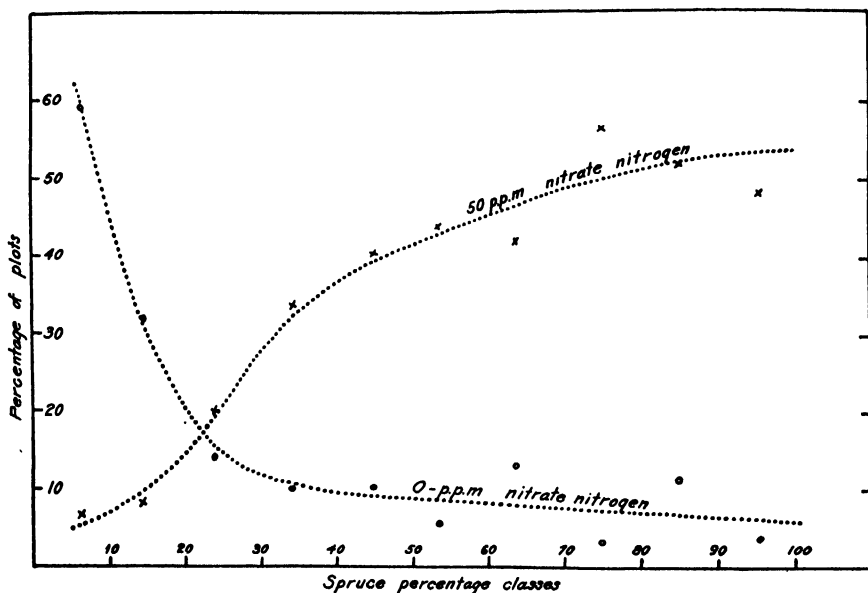


FIG. 2. Relation between soil nitrate nitrogen and spruce percentage. The distribution of plots having (1) 0 p.p.m. nitrate nitrogen, and (2) 50 + p.p.m. nitrate nitrogen indicated with reference to 10 spruce percentage classes.

cent of the plots in the 0–9.9 spruce percentage class had zero p.p.m. but only 10 per cent of those in the 40–49.9 class. In contrast but 5 per cent of the plots in the 0–9.9 spruce percentage class had 50 p.p.m. of nitrates while over 50 per cent of those in the 70–79.9 spruce class showed this amount.

## Relation of Spruce Percentage to Ammoniacal Nitrogen

The successful regeneration of spruce being dependent upon nitrate nitrogen to the extent shown in the foregoing discussion, a lack of nitrates in the
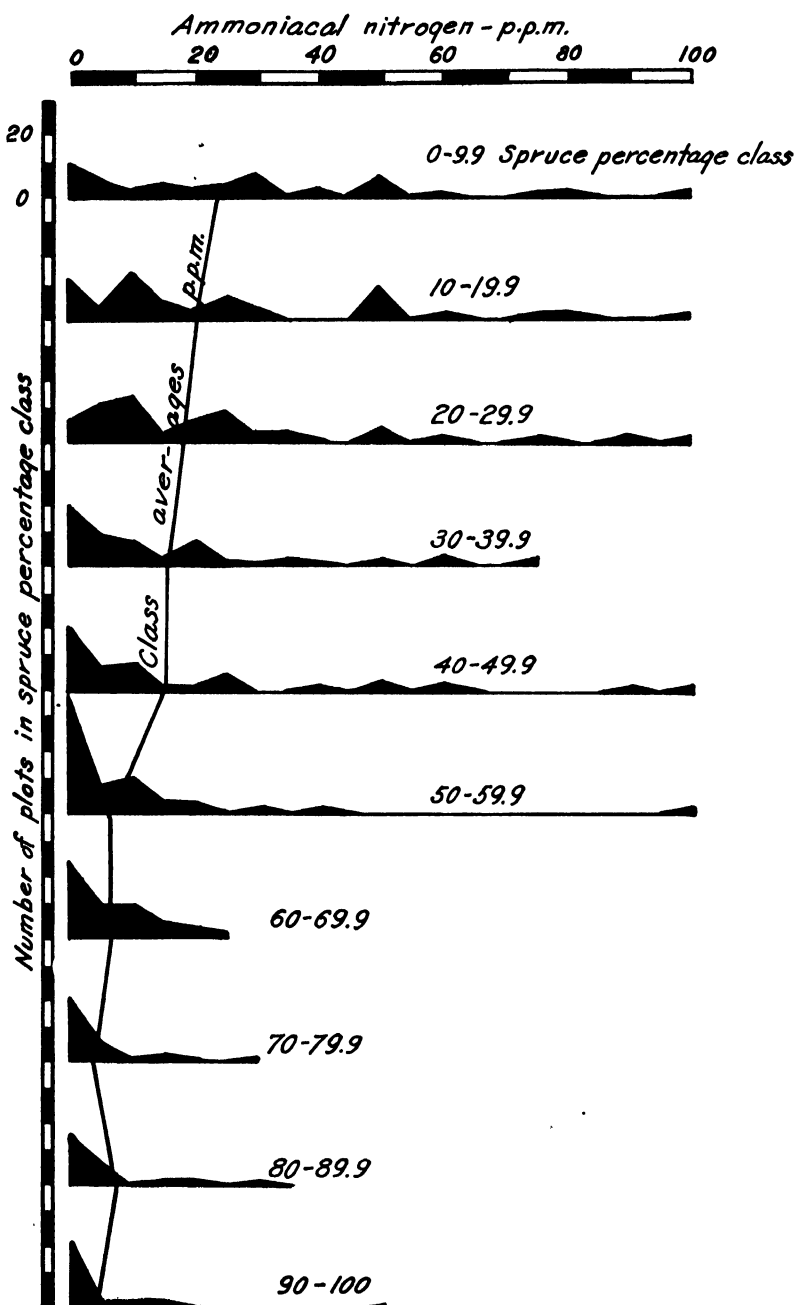
FIG. 3.   Relation between soil ammoniacal nitrogen and spruce percentage.   The distribution of plots with reference to ammoniacal nitrogen indicated for each of 10 spruce percentage classes.

soil should prove an inhibiting factor. Inasmuch as a lack of nitrates in the seedbed samples all containing abundant organic material implies either a total lack of decomposition or that the process has halted with the formation of ammonia, tests for the latter were made. The results indicated that the percentage of spruce decreased with an increase in ammoniacal nitrogen, as shown in figure 3.

The range in quantity of ammoniacal nitrogen in each spruce percentage class, the number of plots in each ammoniacal nitrogen class and the average line are shown in the same manner as in figure 1. The range in number of plots having nitrogen in ammoniacal form is significant. Large percentages of spruce seemingly never occur on seedbeds in which the ammonia fails to be oxidized to nitrate form.

### Relation of Ammoniacal Nitrogen to Nitrate Nitrogen

The above discussion has shown that nitrates do not occur in large quantities with ammonia. If conditions are favorable for oxidation to nitrate nitrogen, the ammonia is transformed immediately upon formation. Where conditions are unfavorable for oxidation, nitrates cannot form but ammoniacal nitrogen accumulates. Consequently with large amounts of nitrates small amounts of ammonia are to be expected. Figure 4 indicates the relationship. This graph is similar in all respects to those of figures 1 and 3. It is seen that 50 p.p.m. of nitrate nitrogen, the saturation point of figure 1, is seldom found where ammonia forms more than 20 p.p.m. and even more rarely where it forms 60 p.p.m.

### Relation of Nitrate Nitrogen to pH Value of the Soil

Clarke ('24), it will be remembered, believed the formation of nitrates was affected somewhat by acidity, as the ammonia was greatest in acid soils, according to his experiments. Aaltonen ('26) noted that ammoniacal nitrogen increased with increased acidity and that nitrate nitrogen increased with a decrease in acidity. Romell and Heiberg ('31) and Lunt ('32) also found a positive correlation between acidity and nitrification.

In this investigation the plots were grouped by pH values and classified according to nitrate and ammoniacal nitrogen, but no relationship was observed. A suggestion of relationship was observed, however, in the analysis of vegetation in one case, and of nitrate values obtained before incubation in another. In the first instance a tendency was noted for *Vaccinium ovalifolium* and *Cornus canadensis*, two raw-humus plants, to decrease in frequency with a decrease in soil acidity. The two species increased in frequency with an increase in ammoniacal nitrogen. Ammoniacal nitrogen increases with a decrease in nitrate nitrogen (fig. 4). Therefore, it is evident that pH and nitrification in the soil are related, although the data of this study did not show it directly.

In the second instance the pH values were compared with the nitrate nitrogen values obtained before incubation. As these nitrate values were small, the plots were grouped into 3 divisions; those having zero p.p.m., those having 1–5 p.p.m., and those having more than 5 p.p.m. of nitrate nitrogen. It was found that 252-plots had zero nitrates and an average pH of 5.04; 154 plots had 1–5 p.p.m. nitrates and an average pH of 5.28; and 92 plots had 5 + p.p.m. nitrates and an average pH of 5.47.
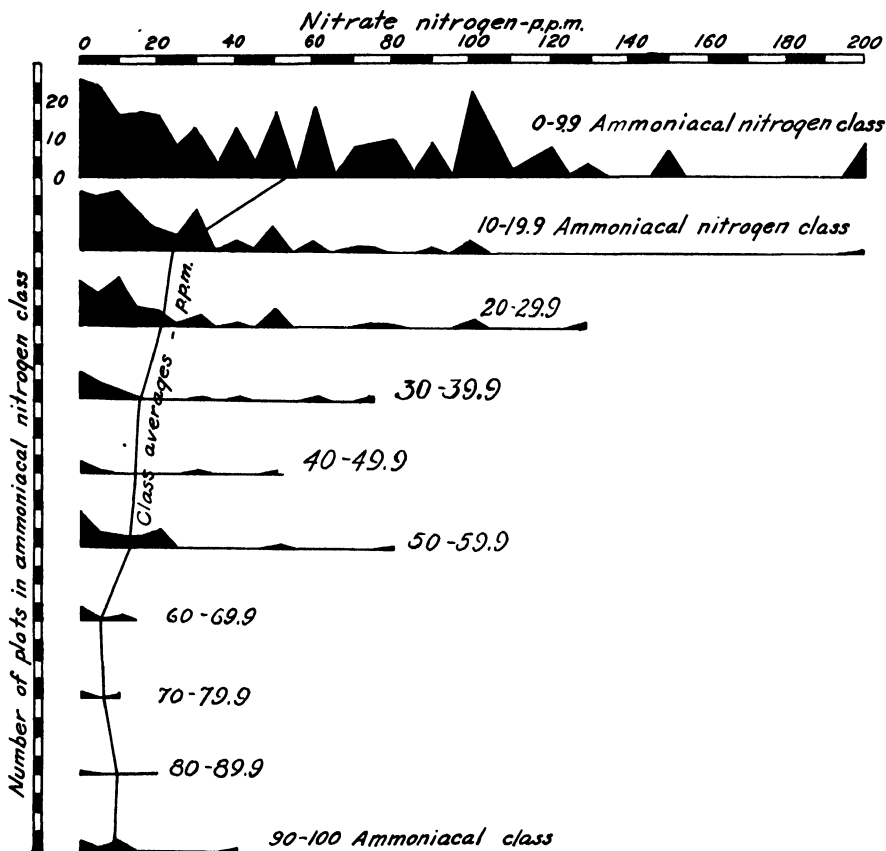


Fig. 4.  Relation between soil nitrate nitrogen and ammoniacal nitrogen. The distribution of plots with reference to nitrate nitrogen indicated for each of 10 ammoniacal nitrogen classes.

It is difficult to compare pH values with nitrification values as both alter rapidly in the field. They cannot be compared following incubation as the process of decay in storage tends to alter the pH, as brought out by Romell and Heiberg ('31) in connection with the decomposition of duff types on cut-over land. These, they stated, changed morphologically, becoming more like mull.

A phase of the work with pot cultures may properly be described here as illustrative of this change.

TABLE II. *Soil reaction of five seedbed types before and during incubation*

| Soil | Before incubation | On 7th day | On 14th day | On 21st day | On 28th day |
|---|---|---|---|---|---|
| No. 1 | pH 4.6 | pH 5.8 | pH 7.0 | pH 7.0 | pH 7.0 |
| No. 2 | 7.4 | 7.4 | 8.0 | 8.0 | 7.6 |
| No. 3 | 6.4 | 7.0 | 8.0 | 7.2 | 7.2 |
| No. 4 | 4.4 | 4.8 | 6.4 | 7.0 | 6.8 |
| No. 5 | 3.8 | 4.8 | 6.2 | 7.0 | 6.4 |

## POT CULTURES

*First Series.* All the seedlings grown in the pot cultures developed normally and for this reason no conclusions regarding them could be reached. All were of approximately the same size with respect to shoot and root length.

The testing of the check pots over a 10-month period resulted in establishing the seedbed types in a definite order according to their power of nitrification. As the quantities of nitrates produced in the open were small, the check pots were placed in a warm room for 10 days to hasten nitrification following completion of the open-air tests. Tests at the close of this period of incubation resulted in a slight alteration of the order of nitrifying power. The two groups are shown in decreasing order of nitrifying capacity:

| *During season* | *After 10 days incubation* |
|---|---|
| 1. *Rubus spectabilis* mull | 1. Alder mull, glacial |
| 2. Alder mull, glacial | 2. Alder mull |
| 3. Sambucus mull | 3. *Rubus spectabilis* mull |
| 4. Alder mull | 4. Spruce duff |
| 5. Spruce duff | 5. Sambucus mull |
| 6. *Fatsia horrida* mull | 6. Willow-poplar mull |
| 7. Willow-poplar mull | 7. *Fatsia horrida* mull |
| 8. Hemlock-vaccinium duff | 8. Hemlock-vaccinium duff |
| 9. Hemlock duff | 9. Hemlock duff |
| 10. Rotten wood | 10. Rotten wood |

The small amount of nitrate nitrogen formed in the pot cultures (fig. 5) during most of the period is attributed to the low temperatures during the growing season, throughout which unusually cloudy weather prevailed. The lack of correlation of nitrate formation with temperature change is believed to be due to the small amount of such change for any extended period. In a climate such as that of Southeastern Alaska, an investigation of the relationship between nitrate nitrogen formation and soil temperature should be conducted indoors under controlled conditions.

According to Weaver and Clements ('29) most soil bacteria do not become active until temperatures of 45° to 50° F. are attained. Temperatures of 65° to 70° F. which make possible good root growth also promote such changes as the decomposition of organic matter with production of ammonia

and the formation of nitrate nitrogen. In one experiment extending over three weeks, Russel (Weaver and Clements, '29: p. 203) found the amounts of nitrates produced at 44°, 94° and 111° F. were 4, 47 and 11 pounds per acre, respectively.
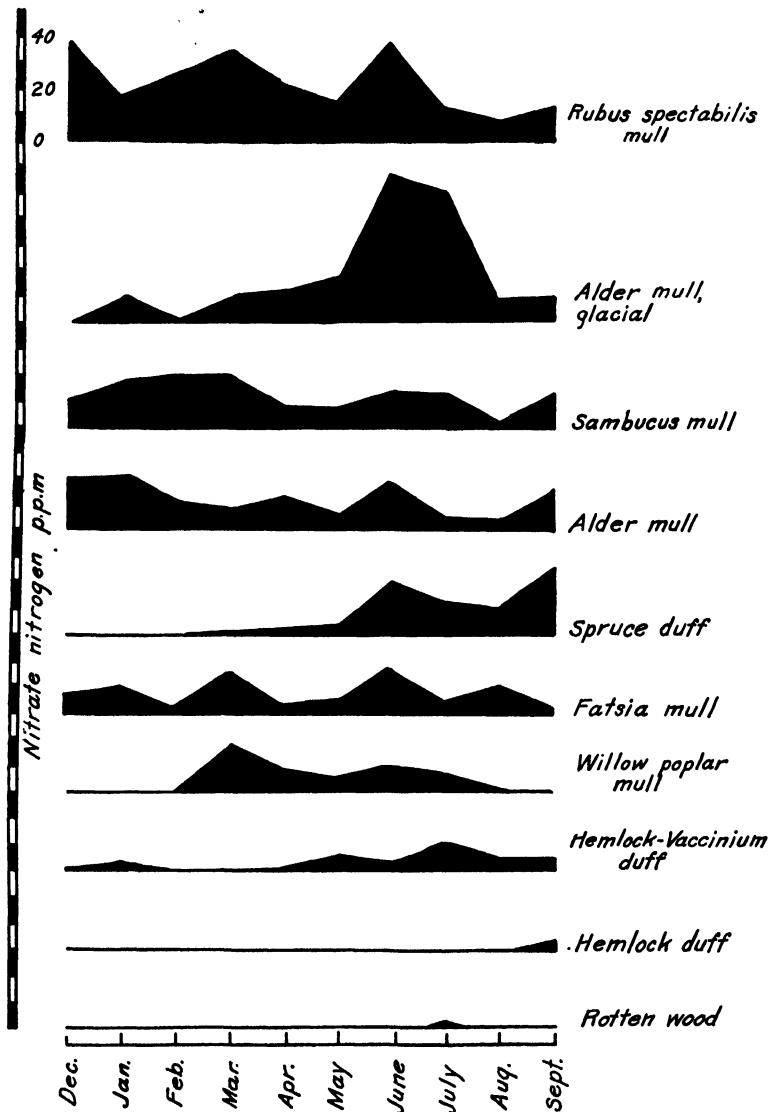


FIG. 5. Nitrate nitrogen formation in various seedbed types. First series of pot cultures.

The results of nitrification tests of rotten wood which failed to nitrify during incubation are in agreement with the findings of Hesselman ('27), who stated that old decayed wood produced weak plants with poor mycorhizas.

With respect to these results, Hesselman explains that decaying wood is of a changeable character and the more completely decayed humus-like decomposition product is decidedly more acid and less favorable to growth than that which still retains its woody structure. In this investigation seedbed material composed of rotten wood was of the pulpy, humus-like character; thus the lack of nitrification agrees with the findings of Hesselman.

Average values for all sample plots having over 50 per cent of their surface covered by rotten wood are: 9 per cent of spruce, 6 p.p.m. of nitrate nitrogen, 19 p.p.m. of ammoniacal nitrogen and a reaction of pH 5.17. They therefore compare with the rotten wood of the pot tests in having very low ability to form nitrate nitrogen. Final ammonia tests show that only three seedbed types contain nitrogen in this form, namely the hemlock-vaccinium duff, rotten wood and hemlock raw-humus.

*Second series.* The results secured in the first series as shown in figure 5, while indicative of certain differences in capacity and speed in nitrate formation when charted by monthly averages, were rather erratic when considered from week to week. In order to avoid this, which may have been due to changes in temperature in the open, the second series was run indoors at a constant temperature of 72° F.

In this series of tests 5 seedbed types exhibiting largest differences in nitrification capacity were selected from those used in the first series and new samples procured. Daily tests at a set hour gave excellent results, confirming the order of nitrification established in series one. In addition to these daily tests, smaller samples of the same seedbed material were incubated for 2 months and tested at the end of that period. These results further substantiated the previously established order of nitrifying power (table III).

TABLE III. *Nitrate and ammoniacal nitrogen content of five seedbed types after two months incubation* [1]

| | Nitrate nitrogen in p.p.m. | Ammoniacal nitrogen in p.p.m. |
|---|---|---|
| *Rubus spectabilis* mull | 205 | 0 |
| Alder mull, glacial | 143 | 0 |
| Alder mull | 106 | 0 |
| Spruce duff | 77 | 0 |
| Hemlock duff | 10 | 40 |

[1] Bottles were set up in triplicate and an average of three tests taken. Figures represent average of two sets of tests taken 24 hours apart.

It is interesting to note the increase in nitrate nitrogen formation with each succeeding day (fig. 6). This is evidence that Hesselman's observations concerning unfavorable raw-humus types are very probably as applicable in this region as in northern Sweden. The beginning of nitrification in the pure hemlock duff is significant, since it indicates the part that favorable temperature plays in the process. In the first series this seedbed type was sub-

jected to the relatively low outside temperatures with the result that there was practically no nitrification. The constant warm temperature under which the pot cultures of series two were stored evidently hastened the decomposition and nitrification of this seedbed material.
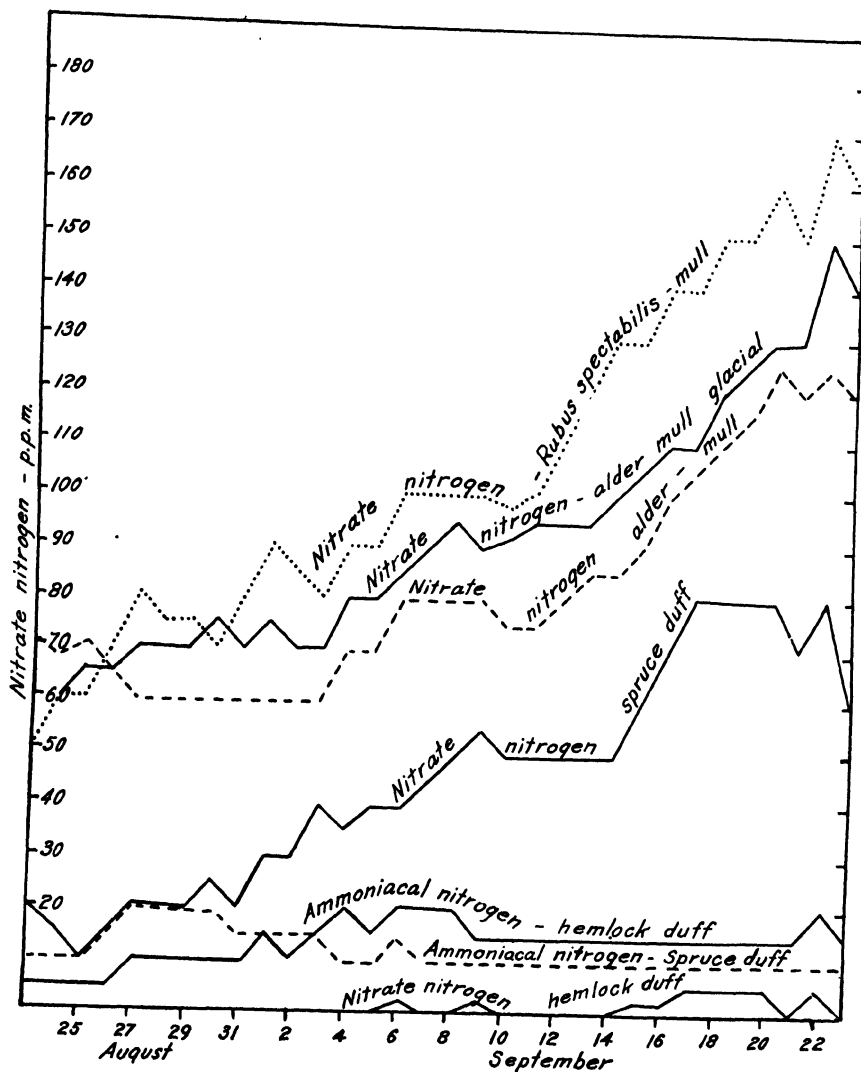


FIG. 6. Progress of nitrate and ammoniacal nitrogen formation in 5 seedbed types during incubation. Second series of pot cultures.

## CONCLUSIONS

Observations over a period of eight years led the writer to believe that seedlings of the two most common tree species in Southeastern Alaska, Sitka

spruce and western hemlock, have different seedbed requirements. The available nitrogen content of the seedbed and the percentage of the two species were thought to be related.

An investigation was carried on by sampling the seedbed on cut-over land and by periodic analyses of pot cultures of certain seedbed types. The specific purpose of the investigation was to determine whether available nitrogen in the form of nitrates or ammonia is an important factor in the occurrence of Sitka spruce and western hemlock seedlings, and to examine the capacity of several of the more common seedbed types to form nitrates and ammonia. As a result of the investigation the following conclusions have been reached:

1. Nitrogen in available form is an important factor in the occurrence of Sitka spruce and western hemlock seedlings. Small quantities of nitrate nitrogen are correlated with low percentages of spruce seedlings. With increasing quantities of nitrate nitrogen comes a marked increase in the percentage of spruce. This does not continue indefinitely, however, but at approximately 50 p.p.m. of nitrate nitrogen a saturation point is reached and thereafter additional amounts of nitrate are not accompanied by higher percentages of spruce.

2. Ammoniacal nitrogen accumulates in seedbeds containing organic material whenever oxidation to nitrates cannot occur. Spruce seedlings are not found in large numbers on such seedbeds although hemlock are abundant. Fifty p.p.m. of nitrate nitrogen, the minimum amount necessary for a large percentage of spruce, is seldom found where ammonia forms more than 20 p.p.m. and very rarely where it forms 60 p.p.m.

3. The power of nitrification varies significantly with the character of the seedbed. The ten seedbed types investigated in decreasing order of nitrifying capacity are: 1. *Rubus spectabilis* mull; 2. Alder mull, glacial; 3. Sambucus mull; 4. Alder mull; 5. Spruce duff; 6. *Fatsia horrida* mull; 7. Willow-poplar mull; 8. Hemlock-vaccinium duff; 9. Hemlock duff; and 10. Rotten wood.

The first four types, as judged by ability to form nitrates, are capable of supporting large percentages of spruce; the other six types are not unless measures are taken to hasten their decomposition and nitrification.

4. The pH values of the sample plots bear little relationship to nitrate nitrogen or ammoniacal nitrogen values which are obtained after incubation, due, it is thought, to morphological and chemical changes during storage. There is, however, a suggestion of relationship between pH and nitrate values obtained before incubation, the acidity decreasing with an increase in nitrates.

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# MOLLUSCAN POPULATIONS OF OLD GROWTH FORESTS AND REWOODED FIELDS IN THE ASHEVILLE BASIN OF NORTH CAROLINA[1]

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The observations here reported form part of a study of the microarthropods of woodland litter made under the Streamflow-Erosion project at the Appalachian Forest Experiment Station, Asheville, N. C. With three exceptions the habitats studied represent new forest growth on land which has been abandoned for agriculture. The general elevation of the area is between 2,000 and 2,500 feet.

Uniform samples of litter were obtained from the different areas studied by means of a steel cylinder made of a four inch length of eight inch steel pipe, one rim of which was ground to a cutting edge. This cylinder was placed on the litter in a typical location and rotated with sufficient pressure to cause it to cut into the litter and humus to the mineral soil. Each sample comprised three cuts made by this cylinder. These three cuts were made within twenty-five feet of each other in litter that was visibly identical. The combined three cuts totaled one hundred fifty-one square inches of surface— roughly one square foot. In no case were mosses, lichens, or herbaceous plants included in the sample. Thus the fauna obtained in the samples fed upon dead leaves, dead wood, or fungi, unless individuals had dropped from the overhanging tree branches, or were introduced by a passing mammal, or were migrating. Collections were made two or three days after rains for the purpose of avoiding arboreal species that might have been washed into the litter. An original set of shells were identified by Mr. E. G. Vanatta.

The leaf mould was thoroughly dried over drying funnels, then shaken and screened through ordinary mosquito netting. The part not passing through the netting was searched without lenses. The sievings were then passed through a standard Tyler 32 mesh sieve to remove the dust and finest debris. Protoconchs and the two whorled shells of such minute species as *Striatura milium* could pass through. The material retained was then spread on a blue card ruled in columns and examined under a dissecting binocular microscope which magnified twelve diameters.

Samples from the following habitats were examined:

1. Old growth cove hardwood forest (northern exposure) at elevation of 2,500 feet. Eighteen species were obtained including nine large species picked

up at random not included in the sample. This is presented as a means of contrast with the old field forest types (now grown on land once cleared for agriculture). Collected September 8.

2. Cut over dry ridge scarlet-black oak forest; rather open canopy; a few pine needles blown in; September 8.

3. Yellow pine hardwood forest; lower layer of litter with dense growth of grey fungus; 70 years old; September 13.

4. Old-field forest, chiefly pitch pine with dogwood understory; 30 years old; September 20.

5. Old-field forest of pitch pine, a hundred feet from sample 4; 30 years old; September 20.

6. Second growth yellow pine hardwoods, burned over in April by a hot fire, destroying all leaf litter; not a quantitative sample; sample taken on ridge with no possibility of introduction of species by washing from higher slope.

7. Control for sample 6.

8. Upper moist slope, cove hardwood forest; burned April of preceding year; not a quantitative sample; seven species recovered in the sample.

9. White pine plantation; closed canopy; thirty years old; October 8.

10. Old-field, short leaf pine; forty years old; growth stagnant; light crowns; isolated stand of one acre in open pasture; litter trampled by cattle; October 15.

11. Old-field pine; uneven aged; dense growth; litter shaded; thirty-five year stand; October 23.

12. Old-field pine; stand of scattered thirty-five year old open grown trees with remaining space taken up by ten year old reproduction; October 30.

13. Conditions intermediate between 11 and 12; October 30.

Table I records the living mollusca secured; dead shells were not counted.

TABLE I. *Molluscan populations in different habitats*

| | Cove | Cove burn | Scarlet-black oak | Yellow pine-oak | Yellow pine-Cornus | Yellow pine | Pine oak burn | Burn control | White pine | Short leaf pine | Old-field pine | Same | Same |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Age of stand | 120· | | 80 | 70 | 30 | 30 | | | 30 | 40 | 35 | 35 | 35 |
| R. carolinensis | 9 | 2 | 2 | 5 | 10 | 8 | 0 | 1 | 3 | 1/1 | 1 | 1/1 | 1 |
| P. pygmaeum | 52 | 9 | 2 | 2 | 1 | 0 | 0 | 1 | 4 | 0 | 1 | 0 | 6 |
| S. milium | 17 | 1/1 | 12 | 20 | 5 | 1 | 6 | 2 | 10 | 1/1 | 11 | 6 | 4 |
| R. cumberlandiana | 0 | 3 | 0 | 1 | 6 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| H. parallelus | 1/1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 |
| Total (per square foot) | | | 16 | 28 | 24 | 9 | — | — | 22 | 1/1 | 13 | 6 | 11 |

By age of stand, with the exception of the first two, is meant the age of the oldest pine tree.   *1/1* indicates a fragment.

## CONCLUSIONS

All the species found in the dry old-field woodlands (as compared to those from the moist cove woodland) have low spires.   Low spires are a better protection than the high spires because the later whorls protect the inner, to which the animal retires during drought.   Thus there is direct correlation between the drought resistance of the species and their occurrence in the more extreme habitat.

*Striatura milium* occurs in all samples, averaging eight (1–20) per square foot.

*Retinella carolinensis* also occurs in all samples but averages only three or four (1–10) per square foot.   In samples 2 and 5 the high number is due to presence of several very young shells which did not pass through the sieves as did the very young of the smallest species.

*Punctum pygmaeum* is less frequent and averages but two per square foot.   It seems to do better in broad-leaf woodland, though locally present in pure pine.

*Retinella cumberlandiana roanensis* and *Helicodiscus parallelus* are occasionally found, and do not seem to be averse to pine land.   They are probably not as easily carried about as the first three species, or may not be able to survive plowing and cultivation.

The average number of adults per square foot is sixteen.   In the one cove sample 108 were secured, representing nine species (though nine larger species were hand picked in ten minutes).

Number of individuals or of species is not necessarily correlated with age of stand.   A sparse population was present in the short-leaf pine stand (sample 10) which had poorest litter conditions, was trampled by cows, and was most open to sunlight.   The white pine stand (sample 9) was dense, not trampled by cows, and had a thick litter layer.   The yellow pine-Cornus stand (sample 4) was fairly dense, had a fair litter layer, but was only 100 yards from an old growth oak forest.

Thus proximity to old growth uncleared forest (for " reseeding ") and amount of shelter available in a stand, are factors favorable to repopulation. Pure pine woodland is not attractive.

Fires seem to have no serious consequences, probably because of the stratum in which the eggs are laid not being seriously affected by the fire.

The food of *Punctum pygmaeum* and *Striatura milium* is probably decaying vegetation or minute fungi of the leaf mould.   This could be definitely determined by examining the stomach contents exposed in microtome sections treated with selective dyes.   Feeding experiments should also be used for obtaining further evidence.

# COMPARATIVE GERMINATION OF TREE SPECIES ON VARI-OUS KINDS OF SURFACE–SOIL MATERIAL IN THE WESTERN WHITE PINE TYPE [1,2]

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In formulating methods for effecting forest regeneration, considerable information is needed as to the germination habits of the species involved. Studies of germination habits have been made for several species in the western white pine type, but heretofore no sufficiently detailed investigation has been made covering the germination habits of all the principal tree species of this type.

To add to the information available on this subject standard greenhouse tests were made with all these species, on surface-soil materials typical for western white pine areas. The physical factors principally considered in controlling the experiment were light, air and soil temperatures, moisture, and relative humidity. The results are presented only as showing the comparative germination of each species tested on the kinds of soil material used.

Use was made of eight sections of forest surface soil, lifted and installed in the greenhouse intact, each of which differed from the others in character of the material forming the upper layer. The surface materials included several kinds of duff.[3] Each of the sections closely resembled the others in quantity and character of sandy loam soil present. The loam was sufficiently deep to act as a reservoir for applied water. making it available to seeds at the sowing depth. As a check, a section of sand was used.

All the soil sections were obtained near Priest River, Idaho, within an area of one-half mile radius and at an elevation of approximately 2,400 feet. The sources of the eight samples represented five common forest subtypes.

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[3] The term "duff," as used in this study, applies to all natural forest-floor materials lying above the mineral soil. Four separate "duff" layers were distinguished: Litter, duff proper, humus, and podsol (leached layer). Of these the first three were present in most of the sections, and the fourth was present in several.

The sections are classified by surface material and character of the stand as follows:

A.  *Undisturbed*

    1. Duff: overmature, partially cut, western white pine stand.

    2. Duff: overmature, virgin, western white pine stand.

    3. Duff: overmature, virgin, mixed stand.

    4. Duff: 80-year-old, second-growth, western white pine stand.

B.  *Disturbed*

    5. Bared mineral soil: 80-year-old, second-growth, western white pine stand.

    6. Ash: 80-year-old, second-growth, western white pine stand.

    7. Duff:[4] overmature, partially cut, mixed stand.

    8. Rotten wood: 80-year-old, second-growth, western white pine stand

The soil sections were placed in cedar flats. All soil sections used were given identical treatment, throughout the experiment.

The seed used in the tests were of the nine species considered to be commercially important in the western white pine type. These are:[5]

| | |
|---|---|
| *Pinus monticola* D. Don | western white pine |
| *Pinus contorta* Loudon | lodgepole pine |
| *Pinus ponderosa* Lawson | ponderosa pine |
| *Pseudotsuga taxifolia* (LaMarck) Britton | Douglas fir |
| *Abies grandis* Lindley | lowland white fir |
| *Larix occidentalis* Nuttall | western larch |
| *Picea engelmannii* Engelmann | Engelmann spruce |
| *Thuja plicata* D. Don | western red cedar |
| *Tsuga heterophylla* (Rafinesque) Sargent | western hemlock |

In each soil section were sown 500 clean, selected seed of the current year's crop of each of the nine species, respectively. Because of the variable characteristics of western white pine seed, and to avoid any influence of the " hold-over " tendencies of seed of this species, 500 2-year-old seed of western white pine, also, were used in each section. Thus the total number of seeds sown was 45,000.

Seed were sown at comparable depths within small compartments in each of the surface-soil sections.

The germination tests were begun January 10, 1933, and were continued for 100 days, ending April 20, 1933. Germination was recorded daily. As the scope of the study did not include survival, all seedlings were plucked when they appeared above the surface.

## RESULTS

The most significant of the results are presented in the accompanying tables I, II, and III.

[4] Disturbance involved in logging had resulted in a thorough mixing of the different duff layers.

[5] Nomenclature is after Sudworth's Check List of the Forest Trees of the United States.

TABLE I. *Germination percentages within 100 days of seed sown, by surface-soil material and species, and viability of seed cut, by species* [1]

| Soil section No. | Surface material, and character of stand | W.H. | E.S. | L.P.P. | W.R.C. | W.L. | D.F. | L.W.F. | P.P. | W.W.P. 1-year seed | W.W.P. 2-year seed | Average germination per cent | Total number of seeds germinated |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Duff: partially cut W.W.P. | 4.6 | 12.2 | 48.6 | 27.6 | 8.8 | 60.0 | 9.0 | 63.6 | 13.8 | 2.2 | 25.0 | 1,252 |
| 2 | Duff: virgin W.W.P. | 23.6 | 15.4 | 52.4 | 63.4 | 40.8 | 78.4 | 9.2 | 56.7 | 20.2 | 1.8 | 36.2 | 1,809 |
| 3 | Duff: virgin mixed | 7.0 | 28.8 | 84.0 | 59.6 | 31.2 | 49.8 | 17.2 | 62.2 | 18.2 | 1.6 | 35.9 | 1,796 |
| 4 | Duff: 80-year W.W.P. | 10.6 | 8.2 | 67.6 | 62.0 | 29.4 | 58.6 | 17.2 | 62.0 | 15.6 | 4.0 | 33.5 | 1,676 |
| 5 | Bared mineral soil | 7.8 | 18.2 | 79.8 | 54.8 | 11.2 | 51.8 | 18.8 | 67.2 | 21.6 | 4.4 | 33.6 | 1,678 |
| 6 | Ash | 11.8 | 9.0 | 75.2 | 36.0 | 30.4 | 74.8 | 27.6 | 71.6 | 35.8 | 10.0 | 38.2 | 1,911 |
| 7 | Duff | 13.8 | 21.2 | 35.2 | 31.0 | 13.2 | 11.8 | 10.4 | 56.8 | 29.0 | 5.4 | 22.8 | 1,139 |
| 8 | Rotten wood | 6.4 | 55.8 | 87.0 | 32.4 | 36.0 | 72.4 | 19.0 | 60.6 | 26.6 | 5.8 | 40.2 | 2,010 |
| 9 | Sand | 13.0 | 17.6 | 65.4 | 18.2 | 22.8 | 35.6 | 11.6 | 61.6 | 21.0 | 3.0 | 26.9 | 1,349 |
| | Average germination per cent | 10.9 | 20.7 | 66.1 | 42.8 | 24.8 | 54.8 | 15.5 | 62.4 | 22.4 | 4.2 | 32.5 | 14,620 |
| | Viability per cent | 22.0 | 93.0 | 96.0 | 79.0 | 48.0 | 87.0 | 67.0 | 85.0 | 97.0 | 86.0 | | |
| | Total number of seeds germinated | 493 | 932 | 2,976 | 1,925 | 1,117 | 2,466 | 700 | 2,811 | 1,009 | 191 | | 14,620 |

[1] Basis of germination tests, 500 seeds in each lot, or 4,500 seeds in all. Basis of viability tests, 200 seeds in each lot, or 2,000 seeds in all.
Initials given represent common names of species as follows:

W.H.—western hemlock      W.R.C.—western red cedar      L.W.F.—lowland white fir
E.S.—Engelmann spruce      W.L.—western larch      P.P.—ponderosa pine
L.P.P.—lodgepole pine      D.F.—Douglas fir      W.W.P.—western white pine.

As table I shows, results of this study indicated that the germination percentages for the nine species as a group are markedly affected by kind of surface material and character of stand. When the nine species are considered separately, the germination percentages of nearly all of them are found to vary even more pronouncedly with these factors. It was impossible to analyze the influences affecting individual lots of seed, as no experimental replication set-up was provided for in the study.

Table II shows that the three surface materials most favorable to germination, according to results with individual species, are ash, duff under a stand

TABLE II. *Surface-soil materials most and least favorable to germination, germination percentages within 100 days for these materials, and viability percentages, by species* [1]

| Species | Material most favorable | | Material least favorable | | Percentage of seeds viable |
|---|---|---|---|---|---|
| Western hemlock | Duff: virgin W.W.P. | 23.6 | Duff: partially cut W.W.P. | 4.6 | 22.0 |
| Engelmann spruce | Rotten wood | 55.8 | Duff: 80-year W.W.P. | 8.2 | 93.0 |
| Lodgepole pine | Rotten wood | 87.0 | Disturbed duff | 35.2 | 96.0 |
| Western red cedar | Duff: virgin W.W.P. | 63.4 | Duff: partially cut W.W.P. | 27.6 | 79.0 |
| Western larch | Duff: virgin W.W.P. | 40.8 | Duff: partially cut W.W.P. | 8.8 | 48.0 |
| Douglas fir | Ash | 74.8 | Disturbed duff | 11.8 | 87.0 |
| Lowland white fir | Ash | 27.6 | Duff: partially cut W.W.P. | 9.0 | 67.0 |
| Ponderosa pine | Ash | 71.6 | Duff: virgin W.W.P. | 56.7 | 85.0 |
| Western white pine | | | | | |
|   1-year-old seed | Ash | 35.8 | Duff: partially cut W.W.P. | 13.8 | 97.0 |
|   2-year-old seed | Ash | 10.0 | Duff: virgin mixed | 1.6 | 86.0 |

[1] Basis of germination tests, 500 seeds in each lot. Basis of viability tests, 200 seeds in each lot, as shown by cutting tests.

of virgin western white pine, and rotten wood. Ash has the highest rating in respect to germination of seed of each of the species western white pine (both 1-year- and 2-year-old), Douglas fir, lowland white fir, and ponderosa pine. For seed of western hemlock, western red cedar, western larch, western white pine (1-year-old), and lowland white fir, the least favorable germination medium appears to be duff under partially cut western white pine.

It was found that the most satisfactory method of rating the surface materials as germination media is comparison of germination percentages of individual species. These comparisons are shown in table III. An alternative method, results of which are presented in the table, is comparison of germination percentages of all species as a group; this is less desirable because the results are influenced considerably by wide differences between individual species in total germination.

The ratings based on germination percentages of individual species show a marked tendency to fall into groups according to whether the soil was disturbed or undisturbed. The three highest ratings went to three disturbed surface materials, namely, ash, rotten wood, and bared mineral soil. The next went to the undisturbed surfaces, in this order: Duff under virgin western white pine, duff under virgin mixed stand, and duff under 80-year-old western white pine. The lowest rating went to an undisturbed surface mate-

TABLE III. *Ratings of surface-soil materials as germination media, on basis of 100-day germination percentages of individual lots of individual species and of all species as a group, and H-ion concentration of surface-soil materials* [1]

| Soil section No. | Surface material, and character of stand | Ratings based on germination | | | | | | | | | | Sum of individual | Final | Rating based on germination percentages of all species as a group | H-ion concentration, in pH units |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | W.H. | E.S. | L.P.P. | W.R.C. | W.L. | D.F. | L.W.F. | P.P. | W.W.P. 1-year seed | W.W.P. 2-year seed | | | | |
| 1 | Duff: partially cut W.W.P. | 9 | 7 | 8 | 8 | 9 | 4 | 9 | 3 | 9 | 7 | 73 | 9 | 8 | 6.08 |
| 2 | Duff: virgin W.W.P. | 1 | 6 | 7 | 1 | 1 | 2 | 8 | 9 | 6 | 8 | 49 | 4 | 3 | 5.96 |
| 3 | Duff: virgin mixed | 7 | 2 | 2 | 3 | 3 | 7 | 4 | 4 | 7 | 9 | 49 | 5 | 4 | 6.20 |
| 4 | Duff: 80-year W.W.P. | 5 | 9 | 3 | 2 | 5 | 5 | 5 | 5 | 8 | 5 | 53 | 6 | 6 | 6.93 |
| 5 | Bared mineral soil | 6 | 4 | 4 | 4 | 8 | 6 | 3 | 2 | 4 | 4 | 44 | 3 | 5 | 7.20 |
| 6 | Ash | 4 | 8 | 9 | 5 | 4 | 1 | 1 | 1 | 1 | 1 | 30 | 1 | 2 | 7.50 |
| 7 | Duff | 2 | 3 | 1 | 7 | 7 | 9 | 7 | 8 | 2 | 3 | 57 | 7 | 9 | 7.66 |
| 8 | Rotten wood | 8 | 1 | 6 | 6 | 2 | 3 | 2 | 7 | 3 | 2 | 35 | 2 | 1 | 4.92 |
| 9 | Sand | 3 | 5 | 6 | 9 | 6 | 8 | 6 | 6 | 5 | 6 | 60 | 8 | 7 | 7.00 |

[1] Best rating is 1, poorest is 9. To compute final ratings on basis of germination percentages for individual lots, ratings for each material were totalled and totals arranged in order from least to greatest. Initials given represent common names of species as in table I.

rial, duff under partially cut western white pine.    Disturbed duff is separated from the other disturbed surface materials.    Sand, the check material, rated next to the lowest.

No direct correlation was found between H-ion concentration of surface material and either total germination percentage or individual species germination percentages.

The results give no indication as to what seedling survival might be expected under the conditions represented in the study.    In determining the composition of timber stands, factors affecting germination are less important than factors influencing survival.

# RESPONSE OF THE PRAIRIE TO THE GREAT DROUGHT OF 1934 [*,1]

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Drought during the growing season of 1934 was the greatest ever recorded in the prairie region. It offered an exceptional opportunity to study the response of native plants to extremely adverse water relations. Measurements of the environmental factors of the prairie, in connection with various grassland researches, have now been completed, except for one year, for the seventeenth consecutive growing season. In a summary of findings at the end of twelve years it was stated that although periods of drought are liable to occur at any time, and especially after midsummer, yet only twice during these twelve years was the water content in the surface six inches of soil reduced to the hygroscopic coefficient, *i.e.* approximately the point where water is nonavailable for growth (Weaver and Himmel, '31). At no time was the available water in the deeper soil entirely exhausted. Drought periods when water was nonavailable in the surface foot occurred during 1931 and 1933 (Flory, '34). Then came the extremely dry summer of 1934 during which the prairie was under the impact of almost continuous drought. These studies were made near Lincoln, Nebraska, but similar conditions prevailed, in general, throughout the tall-grass prairie in the eastern one-third of the state, except in the extreme northeastern part.

## The Spring Drought

After an unusually warm winter with light snowfall, the spring of 1934 began very dry. March had practically no efficient rainfall, a total precipitation of .8 inch occurring in seven different showers. The heaviest shower of April or May was only .24 inch; the total rainfall in April was .35 inch and that of May .49 inch. The arid conditions were accentuated by high winds with an average mean daily velocity of about 12 miles per hour. Frequently these carried great quantities of dust which lodged among the grasses and readily rose again into the air. Temperatures were often abnormally high and much clear weather occurred. The available water. content of the upper foot of soil was sufficient, however, for the early blooming grasses and forbs to make a good initial growth.

*Poa pratensis* developed rapidly, *Stipa spartea, Koeleria cristata,* and

*Elymus canadensis* all grew well during April.   *Carex pennsylvanica, Antennaria campestris, Anemone caroliniana, Cogswellia foeniculacea* and other prevernal bloomers developed vegetatively in about the usual manner.   Their period of anthesis was considerably shortened, however, and the inflorescences somewhat reduced both in number and size (cf. Weaver and Fitzpatrick, '34). Hence, even this earliest aspect was rather poorly developed in the wind-swept, dust-covered, dried vegetation of the previous year.

Many species of the early vernal aspect, which began late in April, developed only poorly, others produced an unusual abundance of flowers and a large crop of seed.   Among the former were *Viola pedatifida, V. papilionacea, Fragaria virginiana,* and *Allium mutabile.*   Species of *Oxalis* grew poorly, *Nothocalais cuspidata* was far below normal, *Vicia americana* had but few blossoms, and *Senecio plattensis* was dwarfed by the low water content of soil and the dry air.   Not infrequently the flowers withered and dried and the production of viable seed was almost nil.   As regards these species, many of which are rather shallowly rooted, the aspect was short and poorly developed.

Conversely the deeply rooted *Astragalus crassicarpus* dominated the aspect, though later the drought of June withered and dried the half-grown fruits.·   *Baptisia leucophaea* blossomed profusely and developed an excellent seed crop.   The culms of *Equisetum laevigatum* formed unusually dense patches of tall stems and the strobili were very prominent.   This species, like the two legumes, extends many feet into the soil (Weaver, '19 and '20). Seed production of *Sisyrinchium angustifolium, S. campestre,* and *Carex pennsylvanica* was also large.

*Poa pratensis* began to bloom with the incoming of the vernal aspect.   Its anthesis was hastened by the drought.   The number of flower stalks was greatly reduced and their height was usually only one-third to one-half normal. In pastures where bluegrass grows in almost pure stands, this species, which is almost entirely rooted in the surface 30 inches of soil, was practically all dried by May 15.   Since many of the annual pasture weeds, such as *Sporobolus neglectus, Schedonnardus paniculatus, Aristida oligantha,* and *Eragrostis major,* failed to germinate, the landscape appeared bare indeed.   But in the prairie where the bluegrass was protected by the shade of other grasses and forbs, most of which absorb at greater depths as well as in the bluegrass root zone, the half-wilted plants remained green until the last of May.   The inability of the invading bluegrass to adjust itself to drought by greatly increasing its osmotic pressure, as do most native prairie species, was well illustrated.   Osmotic pressure of the cell sap increased very gradually from about 15 atmospheres on April 10 to $29A$ when it completely dried on May 25.[2]

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[2] Plant materials were frozen in the field with carbon dioxide ice.   After 18 hours, sap was extracted from thawed material at a pressure of 10,000 pounds per square inch. The freezing point of the sap was determined at once by use of an appropriate thermometer and an ether-evaporation device and the results are expressed in the osmotic concentration of the cell sap in atmospheres $(A)$. ·

The drying bluegrass gave the prairie its early dead appearance; the abundance of this invader could be estimated readily by the color of the landscape; in areas where *Poa* had been killed by two or three years of late burning, the prairie appeared as a continuous carpet of green.

Estival and autumnal forbs, which begin their growth in May and are ordinarily conspicuous because of rapid enlargement, developed slowly under the great evaporation stress resulting from the hot, dry, windy weather. This prevailing conditon was well illustrated by species of *Zizia, Helianthus, Aster, Solidago,* and many others. Moreover, late vernal bloomers were distinctly retarded in their usual activities. *Anemone canadensis* showed wilting, *Galium tinctorium* grew well only where it was protected by the grasses, *Steironema ciliatum* and other species of the lower layers suffered severely from the drought. Certain short-lived, interstitial grasses, such as *Festuca octoflora* and *F. ovina,* failed to appear on the uplands. The shallow-rooted rosettes of *Erigeron ramosus* of the previous summer and fall soon dried, and even the interstitial perennials, in the main, developed poorly, for not only was the soil dry but also the protecting dominant grasses had not made their usual vigorous growth.

## Drought of Early Summer

With the beginning of the estival aspect the last week in May the drought had become pronounced and was accentuated during the first week in June. At this time the spikes of *Koeleria cristata* were beginning to open, and *Stipa spartea* was in full bloom. *Koeleria* is a shallow-rooted grass, rarely exceeding 18 inches in depth. The flower stalks were greatly reduced in numbers and the length decreased from the usual 20 to 30 inches to only 5 to 8 inches. Moreover, the spikes were small and had very little viable seed. By the middle of May the meager foliage was tightly rolled, and the cauline leaves soon died. *Koeleria* had increased its osmotic pressure from about $16A$ in early April to $25A$ on May 10. At the time of drying, ten days later, it had reached $36A$.

The rather deeply rooted *Stipa spartea* occurs in greatest abundance on the ridges in soils not entirely appropriated by *Andropogon scoparius.* As early as the middle of May the effects of drought were evident. The usual 2- to 3-foot vegetative stature was reduced to about 1 foot, and was scarcely exceeded by the flower stalks. Seeds were produced rather sparingly, and very few of them were well filled. The cauline leaves dried much earlier than usual; rolling of the basal leaves began about May 13.

*Panicum scribnerianum* and *P. wilcoxianum,* representative of several interstitial species of minor grasses, blossomed scarcely at all. Instead the half-rolled, wilting leaves showed that the plants were in bad condition. They had made only a poor growth. Drought had not yet greatly affected the dominant bluestems, which are deeply rooted in the subsoil, except that lack of early

rains had resulted in a somewhat sparser ground cover and slower growth. The normal deep green foliage over the uplands was slightly yellowish in color and only 5 to 7 inches in height instead of the usual 8 to 14 inches. The lighter color was undoubtedly correlated with a decreased nitrogen-fixing bacterial activity in the dry soil.

*Antennaria campestris* was among the first forbs to indicate the exhaustion of surface soil moisture. The leaves had rolled early in May and no sap could be extracted from the leaves of plants from the higher slopes after May 10. Their adjustment to drought through increased osmotic pressure was only about 8*A*, a change from 10 to 18*A* in about 20 days. Upon watering plants with withered and dry leaves, they recovered in a few hours as if by magic. The shallow root system of this and certain other species was indicated by lack of recovery when water was applied in trenches at a depth of 2.5 feet.

Quite in contrast was the behavior of *Bouteloua gracilis,* a short grass found only on the driest ridges. The osmotic pressure of 22*A* on May 1 rapidly increased to 42*A* by May 20, and a little later reached the high value of 60*A*. Thereafter no sap could be extracted from this xeric immigrant from the Great Plains. It remained dormant and apparently dead but like *Antennaria* it revived quickly when water in the surface soil became available.

### Water Content of Soil

By the first week in June water content of the soil was greatly reduced and drought had made a deep impress upon the uplands. It was ameliorated temporarily by a .64 inch shower on June 8, and a similar one on the fourteenth. These rains, however, wet the parched soil only to a depth of 3 to 4 inches. A shower of .27 inch and another of .57 inch fell later in the month but any relief afforded was merely temporary. The total rainfall for June was only 2.47 inches. The July rainfall of .4 inch was dissipated in 7 showers.

Depletion of the water available for growth at various depths to four feet is shown in figure 1. Samples were taken in upland prairie from Carrington silt loam on a gentle south slope. The hygroscopic coefficients are as follows: 0 to 4 in., 10.8 per cent; 4 to 12 in., 10.7; 1 to 2 ft., 13.1; 2 to 3 ft., 14.7; and 3 to 4 ft., 13.4 per cent. Examination of figure 1 shows the gradual depletion of the soil moisture at all depths with the progress of the season. Determinations at depths of 5 and 6 feet after midsummer showed that water was continuously available in small amounts at these levels.

### Responses of Grasses and Forbs

By June 7, soil moisture was so depleted on the hilltops and higher slopes that the leaves of *Andropogon scoparius* were tightly folded and a few inches of the tips had dried. In many cases entire leaves had also dried, giving a reddish tinge to the bunches, which were poorly filled and only about half their
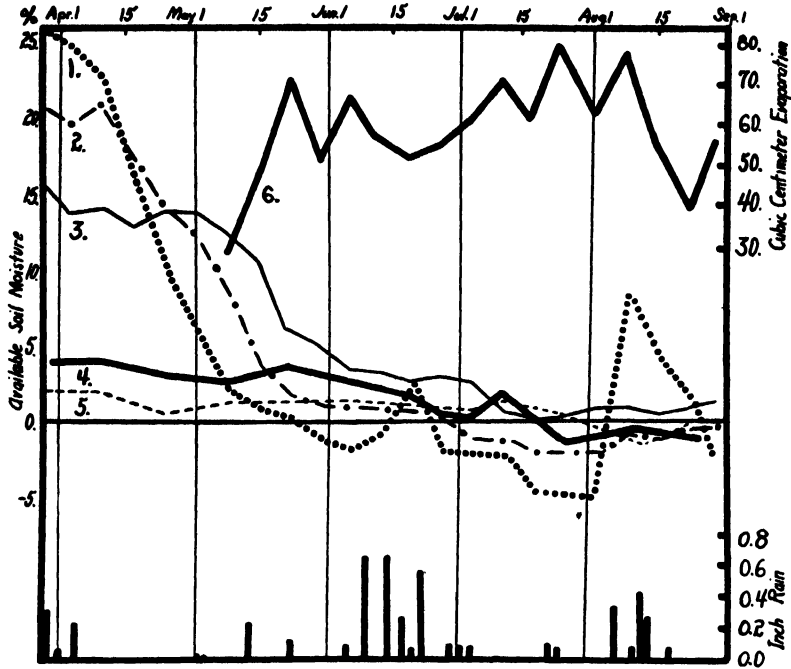
FIG. 1. Water content in excess of the hygroscopic coefficient at (1) 0–4 in., (2) 4–12 in., (3) 1–2 ft., (4) 2–3 ft., and (5) 3–4 ft.; (6) the average daily evaporation by weeks from Livingston's white spherical atmometers; and the rainfall in inches.

normal height. The leaves of *Sporobolus heterolepis* were tightly folded. Leaves of the more deeply rooted *A. furcatus* had begun to wilt, and in the driest places the bluestems had withered and turned brown as if visited by an early frost. *Bouteloua curtipendula* was wilted and the plants greatly dwarfed. *Sorghastrum nutans* showed a wide range of conditions from plants that were entirely wilted to those with folded leaves. Clearly it was in greater distress than the more deeply rooted big bluestem, and appeared to have migrated too far up the slopes during years of abundant moisture (cf. Weaver and Fitzpatrick, '32).

Among the forbs, *Achillea occidentalis* had many dead leaves, half of those of *Solidago rigida* had dried, and *Hieracium longipilum* had much wilted foliage. Late in May the many shallow fibrous roots attached to the thick corm of *Liatris scariosa* could not meet the heavy demands of transpiration and wilting became common, finally recovery by night ceased, and late in June most of the tops died. Quite in contrast was *L. punctata* whose generalized taproot system penetrates the soil to 16 feet or more and absorbs water from a large soil volume. It remained unharmed even on the driest hilltops after all of the grasses were dried. The response of these two species to drought is in striking contrast both as regards their changes in osmotic pressure and re-

tention of water within their tissues. The deeply rooted *Liatris punctata* maintained an osmotic pressure of 11 to 14*A* throughout the growing season, and its water content decreased from 70 to only 56 per cent. The relatively shallow-rooted *L. scariosa* increased its osmotic pressure from 12 to 37*A* and the water content decreased from 72 to 42 per cent.

Few seedlings of any species had started growth and these few were now dead. This was especially noticeable in *Helianthus rigidus* where also young plants from rhizomes had dead or wilted leaves. The stalks of *Delphinium virescens* were greatly dwarfed and the lower leaves dried. *Erigeron ramosus* was badly wilted. The flower stalks were only 6 to 8 inches tall, unbranched or poorly branched, and the flowers were only half the normal size. Blossoming occurred early and was of short duration.

### Effect upon Flower Production

The tendency to blossom early was marked in many species. *Glycyrrhiza lepidota* began blossoming late in May, and *Petalostemon candidus* and *P. purpureus* by the middle of June. The period of flowering in all cases was short. *Solidago glaberrima* had very yellow inflorescences by June 18 and the flowers opened on June 25, fully three weeks early. In general, the prairies were almost without flowers after June 15 and only scantily decorated after June 1. A few of the deeply rooted species (which extend 15 to 20 feet in the moist cool subsoil) produced flowers in extraordinary abundance. Among these were *Psoralea floribunda, Meriolix serrulata*, and *Rosa arkansana*. *Amorpha canescens* began blooming the first week in June instead of the latter part, as usual, but the flowering period was relatively short. *Rosa arkansana*, which normally continues to blossom well into July, had ceased blooming by the middle of June. Both *Silphium laciniatum* and *S. integrifolium* bloomed very early, while precocious plants of *Kuhnia glutinosa* were in flower on July 20.

### Appearance of Prairie Early in June

Over the entire prairie there was a yellowish green tone rather than the characteristic one of deeper green. Since the grasses were short and the interstitial bluegrass dried, the grays and browns of last year's debris showed unusually well as the dry winds whipped the vegetation. The layer of *Psoralea floribunda* had developed well and added a dull green tone. A remarkable feature was the brighter green of the scattered tufts of big bluestem, which absorbs at depths of 6 to 7 feet, contrasting with the reddish-brown bunches of little bluestem, whose roots scarcely exceed 4 feet in depth.

On low ground the grasslands showed little effect of drought, on the slopes they were withstanding desiccation in a remarkable manner, but the thinner soils and drier areas on hilltops and upper slopes were clearly delimited by the drying vegetation.

The unreplenished soil moisture was decreased daily by vigorous absorption by thirsty, half-wilted plants.   The level of available water daily sank deeper.   As drought began its steady and unhindered march down the slopes, responses of the various species to water deficit, as shown by wilting and drying or continuing unchanged, became clearly apparent.

### RELATION OF DEPTH OF ROOTING TO ENDURANCE OF DROUGHT

Among the upland grasses *Andropogon furcatus* was last to succumb since its roots extended deepest.   It remained green long after *A. scoparius*, *Sporobolus heterolepis*, and *Bouteloua curtipendula* were apparently wilted beyond recovery and after *Stipa spartea* had gone into its condition of drought-dormancy.   Where quadrats had been clipped and the surface for transpiration, consequently, repeatedly reduced, big bluestem remained alive above ground many days after the unclipped plants had wilted.   This phenomenon also was clearly evident in many half-deteriorated prairie pastures where, though the soil was moist at a depth of four feet, the dominant bluegrass had dried but the big bluestem and other deeply rooted species continued to draw the precious water.

*Amorpha canescens,* excepting young plants, developed vegetatively as if there were no drought.   It absorbs little in the surface two feet of soil but extends 12 to 15 feet into the cool moist earth.   These plants appeared exceptionally robust because of the low stature of the grasses.   *Kuhnia glutinosa,* with its root system extending 17 feet deep, behaved similarly.   Its only unusual activity was its early flowering.   *Baptisia leucophaea* showed no stress at any time, and like *Amorpha* ripened a large crop of seed.   Its large taproot penetrates very deeply.

*Rosa arkansana,* with a woody taproot often 20 feet long, and younger offshoots closely connected to this main water highway, produced an unusually large crop of fruit and showed no wilting even during the greatest periods of stress.   *Liatris punctata* maintained its foliage unwilted and was of normal stature.   Notwithstanding the adverse conditions, it later flowered abundantly.

The deeply rooted Psoraleas all continued to thrive.   *P. esculenta* seemed unusually abundant.   It blossomed and fruited early and, as usual, the stem broke near the ground line and the plant was blown away.   *P. floribunda* likewise seeded abundantly.   Its efficient, deeply penetrating taproot system furnished sufficient water so that the plants never seemed to be under stress.   The abscission of the stem and the death of the above-ground parts were no earlier than normal.   The species common to lower grounds, *P. argophylla,* completed a normal annual cycle apparently unaffected by drought.

*Aster multiflorus* lost its lower leaves as usual but this deeply rooted plant which holds its water so tenaciously remained green even on the driest hilltops.   The efficiency of the deep, fleshy, but little-branched taproot of *Echinacea pallida* kept this species well supplied with water, except in the case

of young plants.   Both species of *Petalostemon* endured the drought well.
*Solidago rigidiuscula* was a conspicuous survivor and showed a smaller mor-
tality than did *S. glaberrima*.   The latter spreads rapidly and widely by means
of rhizomes.   Well established plants endured, but the mortality among the
younger offshoots was often high.   The large shrub, *Ceanothus pubescens*,
rooted many feet deep, showed no signs of wilting and made green the land-
scape over its entire range from midslope to hilltop.

### RETENTION OF WATER AND OSMOTIC PRESSURES

The graphs of water content of tissues and osmotic pressures of the cell
sap of representative, moderately deeply rooted plants (fig. 2) and very deeply
rooted upland species (fig. 3) show striking differences.   Water content of
the tops of *Andropogon scoparius* decreased from 77 per cent late in April to
52 late in May.   The osmotic pressure showed a somewhat parallel increase
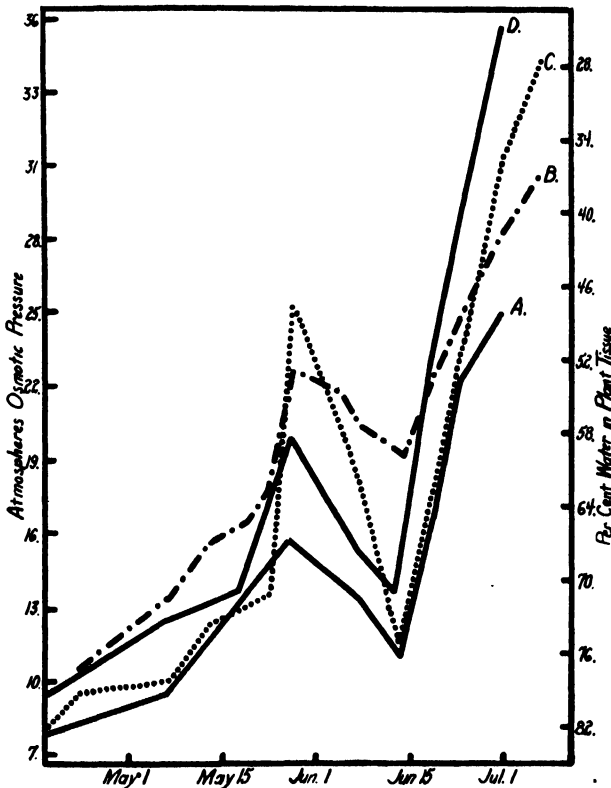


FIG. 2.   Water content of (*A*) *Helianthus rigidus* and (*B*) *Andropogon scoparius*
from April until the plants had dried.   The temporary increase in water content in early
June is due to showers, both species being well adapted to absorb in the surface soil.
(*D*) and (*C*) show the osmotic pressures of the cell sap of the two species, respectively.
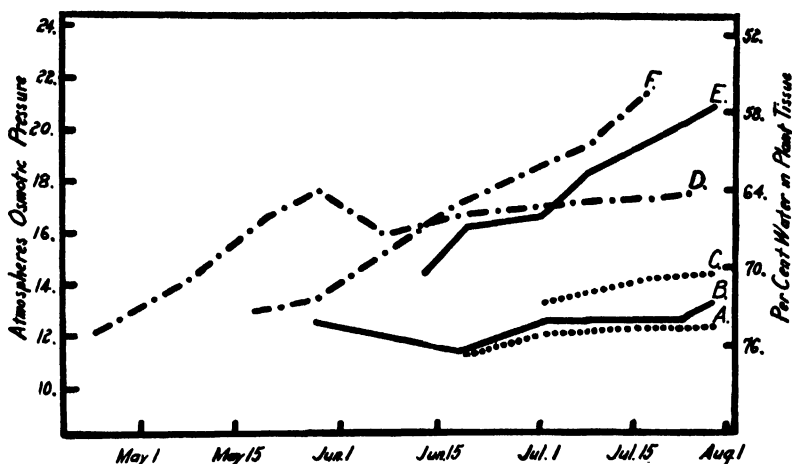
FIG. 3. Osmotic pressures of (*A*) *Kuhnia glutinosa*, (*B*) *Liatris punctata*, and (*D*) *Psoralea floribunda*, all deeply rooted upland plants. Water content of tissues in the same sequence is shown in graphs *C*, *E*, and *F*.

from 8*A* to 25*A*. A rain of .64 inch early in June, which wet the soil only 3 to 4 inches, increased the water content to 59 per cent and reduced the osmotic pressure to 12*A*. With the continued depletion of the subsoil moisture, however, the water content within the plant was decreased to 36 per cent. The osmotic pressure rose rapidly to 35*A* before the tops died. The parallelism between the decreasing water content and increasing osmotic pressure is very similar in *Helianthus rigidus* as is also the response to the increased surface soil moisture due to the June rain. The tenacity with which both species persisted after weeks of semi-wilting was impressive.

The deeply rooted species showed a more complacent existence, for water was to be had, even if in small amounts, from all levels in the subsoil (fig. 3). This available subsoil moisture may be completely utilized by a crop of alfalfa over a period of ten or more years, but in scores of trenches dug in the tallgrass prairie in excavating roots, a dry subsoil under a cover of natural vegetation has never been encountered. Neither water content of the tissues of *Kuhnia glutinosa* nor its osmotic pressure changed to any marked degree. Although the water content of the above-ground parts of *Liatris punctata* decreased from 70 to 56 per cent, the osmotic pressure remained nearly constant, and the plants showed no wilting. Osmotic pressure of *Psoralea floribunda* during June and July was remarkably constant despite the severity of the drought. It is entirely possible that the gradual decrease in water content of tissue from 72 to 56 per cent is a natural physiological process in this species, which gradually develops an abscission layer near the ground line during July.

Among the deeply rooted and consequently unwilted species of lower slopes some of the more important were *Artemisia gnaphalodes*, *Asclepias tuberosa*, *Glycyrrhiza lepidota*, *Silphium integrifolium*, and *S. laciniatum*. None suf-

fered from wilting; flowering and seed production proceeded apparently in a normal manner, except that they were earlier than usual. *Salvia pitcheri*, even when it occurred on higher slopes, also withstood the ravages of drought in a remarkable manner. All these deeply rooted species persisted until fall.

That the wilting and drying of the prairie plants was not due to the high temperatures and low humidities alone, but primarily to low water content of soil was shown in many ways. *Helianthus rigidus*, for example, was often completely wilted and the leaves dried even in the big bluestem sod, while a foot or two distant in cultivated land, the same species was 3 or more feet tall, abundantly supplied with flower heads and entirely turgid. In the main, this species held out well until early July, the wilted plants with leaves half folded persisting for a long time. Finally, many succumbed to the drought. Where local areas in the prairie were heavily watered, not only the revived grasses but all of the forbs as well continued throughout the hottest and driest period without noticeable wilting. The grasses renewed growth, several proceeded to blossom. Forbs that could not be found elsewhere reappeared together with numerous seedlings. Some that had ceased blossoming burst forth in full bloom. The osmotic pressure and the water content of the newly grown tissues of both grasses and forbs were approximately those of the same species before the occurrence of the drought.

## THE MIDSUMMER DROUGHT

The most trying period began about June 20. Before its advent the tops of many species were almost entirely wilted, some had dried. Chief among these were *Drymocallis agrimonioides, Anemone cylindrica* (except on the lowest ground), *Comandra umbellata, Mesadenia tuberosa, Gentiana puberula, Achillea occidentalis, Physalis lanceolata,* and *Erigeron ramosus.* The half-cured little bluestem of hilltops and xeric slopes crunched like snow under one's tread, and the local areas of grama grass were completely dried. Even the accompanying big bluestem was half dried. Then followed a period of most intensive drought. A terrific heat wave swept over the prairie. It continued until the last week in July. During this period the scorching sun seared the prairie as if by fire, and life in all but the most deeply rooted species retreated underground.

### Environment During the Most Intense Period of Drought

In figure 4 it may be seen that the average daily maximum temperature increased week by week from 88° F. to 111° F. The average day temperature (6 A.M. to 8 P.M. inclusive) ranged upward from 77° F. to over 100° F. Even the average daily minimum temperature ranged mostly between 70° and 78° F. Accompanying these extreme temperatures was an average day humidity (including the 8 P.M. reading) that decreased from 48 to only 23 per cent. The average daily maximum humidity exceeded 70 per cent only

early in the period but finally decreased to 40 per cent.  The average daily minimum humidity over a period of six weeks did not exceed 22 per cent and it was as low as 15 per cent.  On some afternoons the humidity decreased to 5 per cent and once to 3 per cent.
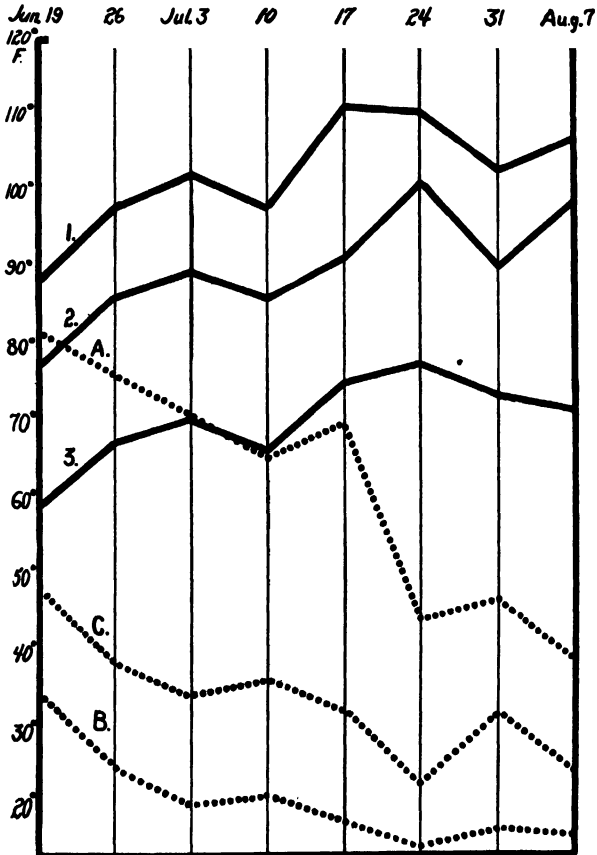


FIG. 4.  Temperature and humidity during the most intense period of drought.  (1) Average daily maximum temperature, (2) average day temperature, and (3) average daily minimum temperature by weeks.  (A) Average daily maximum humidity, (B) average daily minimum humidity, and (C) average day humidity by weeks.  Degrees F. and per cent relative humidity are represented by the same scale.

Accompanying these extremes was an available water content exhausted to the one-foot level with a very dry subsoil at the beginning of the period and to four feet at the end.  Wind movement was often high, averaging over 10 miles per hour during July.  Rates of evaporation (fig. 1) were often twice and sometimes nearly three times as great as those recorded in the prairie during the three preceding years (Flory, '34).  These are the factors that intensified the drought.  Where the water supply was maintained no injury

was done although water loss from a single square foot of the little bluestem vegetation, which was only 5 to 6 inches tall, was sometimes 1.5 pounds per day.

No rain fell; clouds were rare, in fact during the latter half of the period they seldom formed. · The light was intense, the dust-filled, yellow, western sky in evening portending another day of drought.  The hot southerly winds blew as from a desert; drought that had bleached the green hilltops to patches of brown alternating with white, now crept down the slopes.  In pastures and fields great cracks had formed in the soil, increasing greatly the surfaces for soil moisture evaporation and furnishing ready escape for the water vapor diffusing from the soil, perhaps at a depth of 2 to 3 feet.  But in the prairie, because of the unmodified soil structure held by roots and rhizomes and covered with a mantle of vegetation, no cracks were observed.  A 14- to 18-inch *A* horizon sealed over the great network of open spaces surrounding the columns formed in the *B* horizon by the shrinking of the deeper soil of higher clay content.

### Appearance of the Prairie in July

By. the middle of July the tops and drier slopes of the prairie-covered hills appeared almost as dry as the bluegrass pastures.  A week later the area of dried grasses had extended well down the slopes, those facing westward and southward becoming nearly as dry as the uplands.  The advantages of areas such as ravines that had received run-off water to wet the soil the previous year were outstanding.  Even on the lower slopes and in the ravines the deeper greens of May had been bleached to the yellow green characteristic of drought.  On north-facing hillsides the belt of green extended upward only a little way.

Little bluestem was practically all dried on the uplands.  *Sporobolus heterolepis* had yielded a little slower, its greater drought resistance being shown not only by its striking yellow-green bunches among the dried bluestem but also by its rapid recovery through basal leaf growth upon watering.  The little bluestem when watered produced an entirely new crop of foliage.  A few tightly rolled green leaves persisted in the bunches of *Stipa spartea*.  In this respect it resembled *Agropyron smithii*, which occurred very sparingly.  Both of these species unrolled their leaves and revived quickly upon watering.  *Koeleria cristata* was entirely dried as was also *Bouteloua curtipendula*.  *Agrostis hyemalis* and *Eragrostis pectinacea* did not bloom.  *Sorghastrum nutans* had succumbed and also, among the last, *Andropogon furcatus*.

The persistence of the grasses and forbs was remarkable.  *Silphium laciniatum*, although attaining only half its normal stature, blossomed on some uplands.  In societies of *Coreopsis palmata* the dwarfed plants were half dead.  *Aster sericeus* was defoliated to near the top, but species of *Acerates*

seemed unharmed. *Euphorbia corollata* retained only a few of its upper leaves, in some cases all had fallen, yet the dwarfed plants continued to bloom. Only after days of wilting and rolling or folding of the leaves, weeks of battling the intense heat, high winds, and low humidities under the cloudless skies did life finally retreat underground to await the advent of rain. The bronzes, yellows, and golds, colors normally appearing late in autumn, were of short duration. For soon the blazing sun had scorched the withered grasses until the prairie had the bleached appearance common to the late winter aspect. The plants appeared dead and brown, and when walked upon quantities of the dust brought in by early wind storms arose from them.

Unlike a field of maize, wheat, or clover which can sometimes be ruined by a few days of severe drought, the native forbs yielded only a little each day. Neither were their leaves torn and frayed by the wind as were those of cultivated crops. There were no blossoms to tell the seasonal aspect for the oven-like heat and dryness prevented flowering. Many square meters were without a living green thing.

As the weeks passed without rain, even the lowlands began to reveal the impact of drought. By August 5, at the end of the continued heat wave, the bluestem grasses had lost their green color and were wilted and dried even on the lowest slopes. This indicated that the water supply within reach of the roots was practically exhausted even on the low ground. The progress of drying of the big bluestem is of interest. First the two or three basal leaves of a plant turned brown and died. Simultaneously or a little later the remaining leaves died at the tip and then progressively towards the base as drought increased. This grass had nowhere attained its usual 18 to 24 inches in height and was only 9 to 11 inches tall. With the drying of the foliage of the big bluestem, much dwarfed specimens of *Panicum virgatum* and *Elymus canadensis* that had migrated outward too far from their proper place fringing the *Spartina michauxiana* communities in the ravines, showed great distress. The tenacity with which *Panicum* persists, even on uplands where it has become established in disturbed areas, is remarkable. But it and the marginal slough grass were now bleached yellowish green and were about to dry. *Panicum virgatum* possesses the deepest root system of any of the grasses of the tall-grass prairie. *Elymus,* which is only moderately deeply rooted, had, in general, developed poorly.

Many species at home on these usually moist slopes were breaking under the drought. *Hieracium langipilum* began drying while in early bloom with its flower stalks only one-third elongated. *Rhus toxicodendron,* fully exposed to the sun because of the scanty growth of grasses, was burned and the leaves dried and bleached. *Equisetum laevigatum* had lost half its stems, which bleached white in the sun, and the remainder were drying at the tops. *Meibomia illinoensis,* although in fruit, was rapidly drying except in the most favored places as was also *Lespedeza capitata. Helianthus grosseserratus,* spreading outward from its strongholds in the ravines, was greatly dwarfed

and wilted. This was true also for other marginal species such as *Heliopsis scabra, Helianthus tuberosus, Monarda fistulosa,* and *Teucrium canadense.* A few species, such as *Vernonia baldwini, Asclepias sullivantii,* and *Silphium integrifolium,* grew normally and stood unwilted above the dried grasses.

The very slow decrease in the water content of the tissues of representative forbs and grasses, all deeply rooted in the formerly wet soil of the ravines, is shown in figure 5. The average decrease from early spring to August 1 was from about 80 to 60 per cent. The osmotic pressure showed even less change, increasing only 2 to 3$A$ from April to June, and 1 to 2$A$ more by August 1. These slight changes would probably also characterize upland plants during normal seasons with plentiful soil moisture.
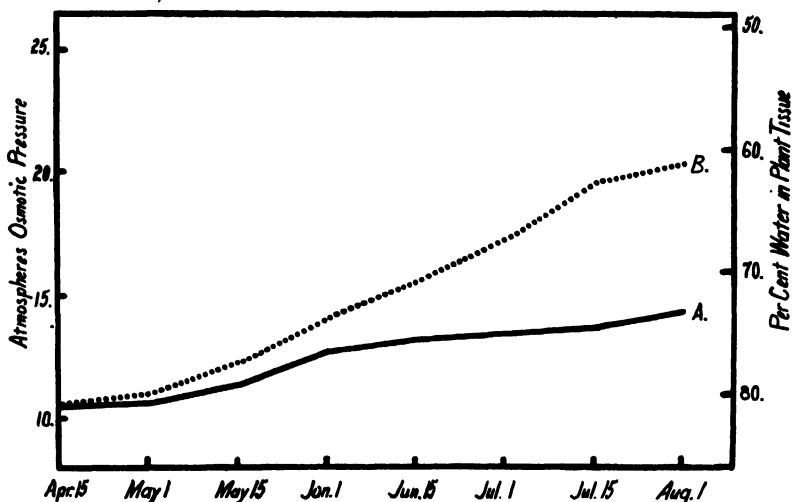


FIG. 5. (*A*) Average osmotic pressure and (*B*) average water content of five species of lowlands, viz.: *Helianthus grosseserratus, Aster salicifolius, Solidago altissima, Panicum virgatum,* and relict *Spartina michauxiana.*

The drought also left a deep impress upon the vegetation in slough-grass alternes and wetter areas of the ravines. On the Belmont prairie, for example, the water table had been lowered by the first week in August to 5.5 feet where normally it is at or near the soil surface. Although *Phalaris arundinacea* was only half dried, alternes of *Carex vulpinoidea* were burned brown. *Carex* had undergone a reduction in water content of tissues from 69 to 33 per cent, and an increase in osmotic pressure from 12 to 41$A$. The decrease in water content of *Phalaris* was from 80 to 60 per cent, and the osmotic pressure increased from 14 to 22$A$. *Scirpus atrovirens* was half dried and had produced no seed. *Spartina* was dwarfed, the ends of the leaves were brown, and the plants with rolled leaves were half dried. In relict patches of *Typha latifolia,* the plants, which had headed at about 4 feet, were so dry that scarcely any green tissue remained. Their osmotic pressure

rose from 6 to 19*A* and the water content decreased from 87 to 72 per cent by July 15. The understory of *Leersia oryzoides* was dead and dry. Characteristic swamp species such as *Verbena hastata, Asclepias incarnata,* and *Bidens bipinnata* were wilted even in early morning.

## DROUGHT OF LATE SUMMER

Scattered showers and periods of cool weather mitigated the drought after the first week in August. A rainfall of .36 inch occurred on the sixth, .51 on the twelfth and thirteenth, and the drought was finally ended by 1.33 inches of rain at the end of the month.

### *Behavior of Species on Uplands*

The responses of the grasses, that were not entirely dried above ground, were marked for a few days after each shower. The few green leaves still alive among the bunches of *Stipa spartea* unrolled. But many of the bunches showed no greening. Some leaves in the most resistant tufts and bunches of *Andropogon furcatus, Bouteloua curtipendula,* and *Sporobolus heterolepis* renewed growth at the base. Also a few new leaves appeared. Even some of the most deeply rooted plants of *Andropogon scoparius* began to put forth new foliage. But such greening and growth were not continuous nor did they occur generally. Growth had scarcely gotten well under way before the surface water supply was again exhausted. The persistence of scattered individuals of a species that in general had died above ground was of much interest. A single bunch of little bluestem with a few persistent green leaves, a plant of *Gentiana puberula,* or an individual of *Liatris scariosa* persisting in spite of the drought, are typical examples. One had to observe closely to perceive the new development; the local tone was yellowish green rather than bright green, and both in the uplands and valleys the general bleached aspect of the prairie remained unchanged. *Poa pratensis, Koeleria cristata, Antennaria campestris,* and many other species made no new growth.

The general height of the upland grasses varied from about 4 to 7 inches; in places it did not exceed 3 inches. The cover was conspicuously open, and where spring burning had occurred much soil was bare. The basal cover averaged perhaps 15 to 20 per cent less than normal.

The forbs that had been killed above ground showed little or no renewal of growth. The deeply rooted ones that endured the midsummer drought still remained green, although not the deep green of a moist summer. The deeply rooted upland plants slightly decreased their osmotic pressures late in August, as a result of the increased soil moisture and humidity. Water content of tissues increased very slightly. Less deeply rooted species, that also depended somewhat upon surface soil moisture, were somewhat revived and showed a decrease in osmotic pressures of 6 to 10*A*.

On lower slopes *Asclepias tuberosa* had lost scarcely a single leaf. Gray societies of *Artemisia gnaphalodes* decorated the somber landscape. Others of *Glycyrrhiza lepidota,* brown with ripened fruits overtopped with the green foliage, showed conspicuously above the short growth of dried bluestems. *Vernonia baldwini* flowered early and the inflorescence was dry in late August. *Ceanothus pubescens* still remained green; *Amorpha canescens* lost its lower leaves as is usual in August; *Rosa arkansana* continued functioning as if the year were quite normal; and *Liatris punctata* showed no signs of drought. Among the upland goldenrods, *Solidago rigidiuscula* was affected least; *S. glaberrima* likewise persisted everywhere, but after severe mortality and the loss of lower leaves. *Echinacea pallida, Petalostemon candidus,* and *P. purpureus* also showed great resistance to drought and remained green until late fall. *Meibomia illinoensis* was considerably defoliated. Many wilted plants of *Helianthus rigidus* regained turgidity and survived; they were greatly dwarfed, produced no flowers, and maintained only a few pairs of terminal leaves. *Silphium laciniatum* and *S. integrifolium* bloomed early; the stems were usually short. *Aster multiflorus* persisted even on the driest ridges, as did also *Kuhnia glutinosa* and *Euphorbia corollata,* the last two frequently in great abundance. Often the abundant, showy inflorescences of the flowering spurge alone gave tone to the landscape.

The early autumnal aspect was indeed poor. Scattered throughout were flowers of *Solidago glaberrima,* more abundant ones of the less conspicuous *Kuhnia glutinosa,* and an occasional *Physalis lanceolata* in full bloom. On lower slopes the bright blue flowers of *Salvia pitcheri* occurred but not abundantly, and the yellows of *Oenothera biennis* showed occasionally.

### Behavior of Species on Lowlands

In the ravines the ravages of drought proceeded steadily but slowly. At Belmont prairie near the end of August, saturated soil was found only at a depth of 6.5 feet. Such characteristic species as *Aster salicifolius, Solidago altissima,* and *Helianthus grosseserratus* were developing flower heads on stalks only one-half to two-thirds the height of the dried stems of the previous year. *Helianthus* had lost all but the top 4 to 6 inches of foliage. Some of the plants were wilted. Many species showed by dwarfness, wilting, and drying considerable deterioration since early August.

On the lowlands along the Missouri River, where drought was belated by 4 inches of rain in June, growth had ceased by July 20. After this shortage of water was continuous although the water table under the big bluestem is normally only 7 to 9 feet deep (Weaver, *et al,* '35). In August the foliage of *Andropogon furcatus,* commonly 2.5 to 3 feet high, averaged only 22 inches. Whole meadows appeared semi-wilted; the drying grass rustled as one walked through it. The usual deep green had been replaced by the yellowish greens, reds, and bronzes of late autumn. Scarcely a flower stalk could be found.

Where sandy or gravelly soil replaced the heavy loam, the grass was dead. Plants forming the conspicuous understory began dying early in July and were now completely dried. The most conspicuous were *Fragaria virginiana, Steironema ciliatum, Anemone canadensis, Galium tinctorium,* and *Equisetum arvense. Panicum virgatum* was even more poorly developed than big bluestem. The panicles, which appeared very early, were only 2 to 3 feet tall compared to the usual stature of 5 to 5.5 feet. The foliage was yellowish in color and many leaves were dried. *Elymus canadensis* was reduced proportionately in height. The foliage of *Spartina michauxiana* reached only 3.5 to 4.5 feet, which is a little more than half the usual stature. It had a light green color. The flower stalks, which often reach heights of 7 to 9 feet, were scarcely taller than the foliage.

After the rains of early September the grasses of both uplands and lowlands made some new growth, but the season was too far advanced for much development. Many clumps of several species appeared dead. Numerous permanent quadrats have been mapped so that the further history of the vegetation may be determined during the next growing season.

## SUMMARY

The most severe drought ever recorded in the prairies of eastern Nebraska occurred during 1934. Water content of the upland was gradually depleted, and by July 30 no water to a depth of 4 feet was available for growth. During July the average maximum daily temperature varied from 98° to 111° F. and the average minimum daily humidity from 15 to 22 per cent.

Blossoms of deeply rooted plants marked the vernal and estival aspects. Flowering often began 2 to 3 weeks earlier than normal and was of shorter duration. *Poa pratensis, Koeleria cristata, Antennaria campestris,* and other shallowly rooted species dried in May, developing osmotic pressures of only 18 to 27 atmospheres. *Andropogon scoparius* in the dry upland soils withered early in June; *A. furcatus,* because of its deeper root system, persisted a longer time. *Stipa spartea* and *Bouteloua gracilis* were more resistant, rolling their leaves and assuming a condition of drought-dormancy.

Among the forbs, resistance to drought was closely correlated with root extent. Species with root systems penetrating 8 to 20 feet into the moist subsoil were little affected. Water content of tissues decreased but little with the progress of drought and increase in osmotic pressure was slight. Where the root systems were shallow and less efficient, decrease in water content of tissues was pronounced, and increase in osmotic pressures was 8 to 38*A.* Many species wilted and dried.

Drought swept from hilltops down the slopes into mesic and hydric ravines. Wilting and drying were not due alone to high temperatures and low humidities but primarily to low water content of soil, since plants in watered areas thrived.

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# OBSERVATIONS ON PARAMECIUM DURING EXPOSURE TO SUB–ZERO TEMPERATURES

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## INTRODUCTORY ·

This paper describes the essential details of a simple method for observing microscopic forms during exposure to sub-zero temperatures in an undercooled aqueous medium, together with observations on the influences of the low temperature on one organism, namely Paramecium. The organism may be observed continuously during the time that the temperature of its environing medium is altered from that of the room to one considerably below zero (*e.g.*, — 15° C.), or vice versa.

In a recent contribution, Chambers and Hale ('32) have described observations made upon muscle fibres, an amoeba, and epidermal cells of onion scales during subjection to sub-zero temperatures. Insofar as the present writer can discern, this is the only previous sub-zero temperature study in which the experimental organism (or tissue) has been observed continuously during application of the low temperature. This does not signify, however, that the literature of the biological effects of low temperatures is of limited character. On the contrary, a rather extensive literature is extant; it has been critically summarized in a valuable review by Cameron ('30).

If observations are to be made at sub-zero temperatures upon an organism which normally exists in an aqueous medium, a technique of undercooling this medium must be utilized since, obviously, the organism could not be viewed through the microscope were its environing medium to become solidified and opaque at the sub-zero temperatures. Methods of undercooling which have been employed, and the lowest temperatures to which water has been undercooled by each, may be outlined briefly as follows:

1. The liquid is cooled very slowly in an open vessel, precautions being taken to prevent jarring: limit, — 10° C. (Borovik-Romanova, '24);
2. The liquid is suspended in an oil in the form of a globule, and the volume of oil is then cooled: limit, — 12° C. (Borovik-Romanova, '24);
3. The liquid is cooled at an exceedingly rapid rate: limit, — 17° C. (Hawkes, '29; Young and Cross, '11; Freundlich, '26);
4. The liquid is drawn into a capillary tube and cooled while so enclosed: limit, — 18.9° C. (Borovik-Romanova, '24; Bigelow and Rykenboer, '17).

The objective of the present work, namely the observation of Paramecium during exposure to sub-zero temperatures, was best served by the last-described method. Accordingly, this method of undercooling was adopted.

## MATERIAL, METHODS, AND APPARATUS

The experimental organism employed throughout was a species of Paramecium, either *P. caudatum* or *P. aurelia*. No effort was made to determine the organism more exactly, to culture it in pure line, nor to control culture conditions. The medium was a hay infusion.

The capillary tube method for undercooling was employed throughout. The essence of this method, as herein applied, is simply that the experimental organism is drawn into a glass capillary, together with a volume of its culture medium, and the capillary is then cooled. The capillaries employed were drawn from clean soda-glass tubing; they were of 0.05–0.5 mm. internal bore and 1.5–2 cm. length. The capillary should not be of too great an internal diameter, for the degree to which water may be undercooled in a capillary tube is an inverse function of tube diameter (Bigelow and Rykenboer, '17; Borovik-Romanova, '24) ; nor should it be too small, else it may be narrower than the Paramecium.        In order to imprison a single individual within a capillary, one end of the open capillary tube was lowered into a thin drop of culture medium· (containing Paramecia) close beside any desired individual, which was being followed under low-power microscopic observation; the organism· is thus drawn into the tube, together with some culture liquid, by capillary action. In order to imprison a number of individuals, a capillary was drawn on .25 in. soda-glass tubing, the full-sized end of the resulting " pipette " was filled with the culture, the capillary end of the " pipette " was sealed in a flame, and the " pipette " was suspended in a centrifuge cup and then lightly centrifuged with capillary end outermost; the organisms thus thrown down into the capillary were imprisoned therein by quickly removing the " pipette " from the centrifuge and breaking off the capillary end. After filling, the open ends of capillaries were for a short time left unsealed, in order that evaporation might cause the menisci to retract some short distance. The capillary ends were then capped with paraffin, by carefully applying melted paraffin, carried on some warm metal object, under the view of a low-power microscope. Caution must be exercised not only in order to avoid killing of the imprisoned organism by the heat of the melted paraffin, but also to prevent the opaque paraffin cap from extending over the retracted meniscus and thus obscuring some length of capillary column into which the organism might swim and thus become hidden from view.

The apparatus which was devised in order to cool the organism, and also to observe it microscopically during such cooling, may best be explained with the aid of the accompanying diagram (fig. 1). A brass plate makes contact through its under-surface with two cold-conducting leads, the distal ends of
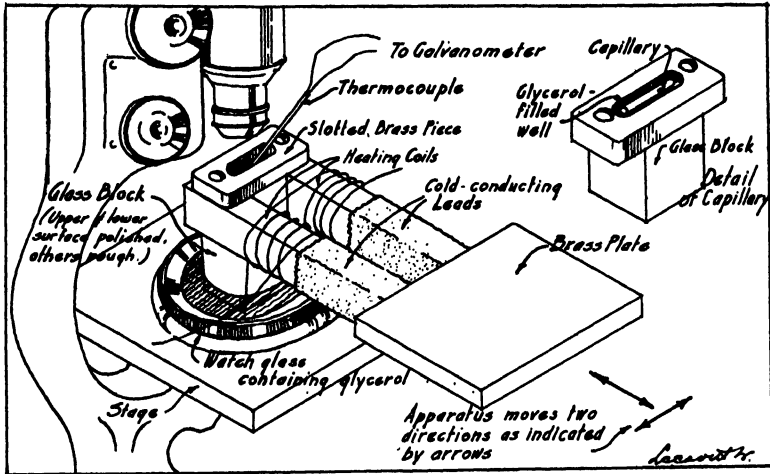
FIG. 1.

which are joined by a slotted brass piece. About the distal quarter-length of each lead, and separated from it by a thin layer of an electrical insulator, is wrapped a line of Nichrome resistance wire; this is used to supply heat whenever desirable. A plate-glass block, of which only the upper and lower surfaces are polished, is cemented to the under surface of the slotted brass piece; this converts the slot into a glass-bottomed well, which can be filled with glycerol, and it is in this glycerol-filled well that the Paramecium-containing capillary is laid, supported by a cross-wire at either end of the well. Cloth insulation was applied to the brass parts wherever feasible, and the Nichrome resistance wire was covered with thin asbestos paper. The whole structure was mounted on a Taylor micro-dissector, in order to afford ready movement in the two directions of the horizontal plane (fig. 1), and arranged so that the slotted piece projected above the stage of a microscope. The lower (polished) surface of the glass block was immersed in glycerol contained in a watch-glass placed on the microscope stage. This glass block cannot frost over when the slotted piece (to which it is cemented) is cooled, for its upper surface is now covered with, and its lower surface is immersed in, glycerol; hence this glass block functions as a non-frosting bottom for the well which has been formed in the slotted piece.

The temperatures to which an organism was exposed were taken continuously by use of a thermocouple, the small, capillary-encased variable junction of which was located [1] in the well, it being assumed that the temperature of

[1] Preliminary experiments indicated that when the temperature of the glycerol well was altered rather slowly (as in the experiments herein recorded) significant temperature gradients did not occur within the well. Hence, the location of the variable junction within the well was a matter of no importance.

the organism within the glass capillary did not differ significantly from that of the environing glycerol.

In order to apply the low temperature, the capillary tube (containing an organism or organisms) was laid in the glycerol well, and a block of " dry ice " (solid $CO_2$) was then placed on the brass plate. Heat is of course abstracted from the glycerol of the well, via the slotted brass piece and the cold-conducting leads, with the result that the organism is cooled. (Temperatures as low as — 50° C. were thus obtainable in the well). Warming was accomplished by removing the " dry ice " block and also by passing current through the resistance wire wrapped about the leads.

The glycerol obviously serves as a refrigerating medium. It was selected for this purpose because of the following characteristics: (1) Low freezing-point; (2) transparency; (3) chemical inactivity toward the paraffin caps of the capillary tubes; and (4) an ability to take up water and thus prevent frosting of the exposed (upper) surface of the well.

An organism imprisoned in a capillary tube was observable microscopically, the micro-dissector being manipulated so as to keep any selected individual continuously within the field of the stationary microscope.

The apparatus just described is objectionable in at least two respects: (1) It does not provide a reproducible time-rate of temperature change, positive or negative, and hence successive individuals cannot be accorded identical treatment; and ·(2) it does not provide a means of maintaining an organism at a pre-determined low temperature.

### EXPERIMENTAL

*1. General Observations on Paramecia Imprisoned in Capillary Tubes* [2]

*a. At Room Temperature.*

Recently imprisoned organisms generally swim about very actively. As time passes, the imprisoned organism tends to become quiescent; but this quiescence is not enforced, and the organism will recommence active movement upon application of some stimulus (*e.g.*, heat). Paramecia do not seem to be harmed in the slightest degree by prolonged incarceration, individuals appearing normal after passing three days within the capillary tube. Any individual Paramecium, whether alone in the tube or accompanied by others, evinces a tendency to locate in direct contact with a meniscus, at either end of the capillary liquid column. The organisms are unable to penetrate this liquid-air interface; some strike at it persistently " head on," as though seeking to break through.

*b. Consequences of Temperature Changes.*

Cooling stimulates quiescent individuals to active movement. As the cooling continues, the velocity of translational motion decreases (p. 635), as is to

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[2] Observations made on Paramecium while enclosed in capillary tubes are recorded by Crampton ('12) and by Kalmus ('29).

be expected; also, the organism generally evinces marked tendencies to swim backward and also to rotate about its longitudinal axis without moving translationally. All organisms cease bodily movements, both translational and rotational, when subjected to sufficiently low temperatures. The cilia generally continue to beat, but they may likewise be stopped at a slightly lower temperature.

Provided that the low temperature exposure has not been of sufficient intensity or duration to prevent, warming induces a resumption of movement. A striking peculiarity, observed in a few instances, is the tendency of the anterior end alone to rotate through a large circle, of a diameter 4–5 times that of the Paramecium itself, as the organism moves slowly forward (described by Jennings, '06, as an aspect of the " avoiding reaction "). •

Morphological degeneration, manifesting itself first as a rounding of the cell, is prone to accompany a low temperature exposure, particularly if it be protracted (e.g., 10° C. for 10–15 mins.). Recoveries following upon restoration of the normal temperature are not uncommon; however, in some individuals the degeneration proceeds rapidly (2–3 mins.) to a complete disintegration. Furthermore, this degeneration and disintegration may occur despite the fact that the individual has resumed apparently normal movement upon being warmed. The morphological degeneration appears to involve an increase of cell volume, as judged by the area of the organism's outline. Individuals injured by the low temperature exposure often display the nucleus to excellent advantage, as they also do when injured by heat or excessive centrifugation.

No individual Paramecium was observed to survive freezing of its environing liquid medium, though Efimoff ('24) reports such survivals; rather, all have appeared misshapen, motionless, and disintegrating.

## 2. Temperatures at which Bodily and Ciliary Movements Cease on Cooling and Recommence on Warming

Observations were made to determine the temperatures at which bodily movements (translational and rotational) and ciliary movements were halted as the temperature descended, and, likewise, those at which these functions were resumed upon warming. The organisms were experimented upon individually, one in a tube. The procedure consisted simply in cooling the organism and in then *immediately* warming it, the desired temperature points being noted as the temperature first fell and then rose. Other data noted were: minimum temperature attained in the cooling process; time of cooling, from + 10° C. to the minimum temperature; time of warming, from the minimum temperature back to + 10° C.; and, abnormalities resulting from the low temperature exposure.

The data obtained are:

TABLE I.  *Effect of temperature upon Paramecium*

| Indi-vidual | Temperature → Descends → | | Temperature → Ascends → | | | Cool-ing time | Warm-ing time | Remarks |
|---|---|---|---|---|---|---|---|---|
| | Bodily move-ments cease (° C.) | Ciliary move-ments cease (° C.) | Mini-mum tem-pera-ture (° C.) | Ciliary move-ments recom-mence (° C.) | Bodily move-ments recom-mence (° C.) | (mins.) | (mins.) | |
| 1 | − 5.3 | − 6.5 | − 8.0 | 5.3 | 10.5 | 10 | 7 | Disintegrated soon after exposure |
| 2 | − 9.5 | — | −15.0 | −1.5 | 1.5 | 10 | 8 | Died soon after exposure |
| 3 | − 7.0 | − 7.7 | − 7.7 | −2.7 | − 2.7 | 8 | 4 | Recovered completely |
| 4 | −14.2 | −14.2 | −16.0 | — | −11.7 | 13 | 5 | Recovered completely |
| 5 | − 6.1 | − 6.1 | − 6.1 | −4.0 | 1.7 | 6 | 5 | Disintegrated soon after exposure |
| 6 | − 2.7 | − 2.7 | − 9.9 | — | 2.0 | 5 | 5 | Recovered completely |
| 7 | − 5.6 | − 5.6 | −10.7 | — | − 1.5 | 8 | 7 | Disintegrated soon after exposure |
| 8 | − 9.0 | − 9.0 | −13.0 | — | − 0.5 | 8 | 6 | Recovered completely |
| 9 | − 6.1 | − 6.1 | − 8.7 | −5.0 | − 5.0 | 6 | 6 | Recovered completely; fission |
| 10 | − 6.1 | − 9.5 | −11.7 | −2.7 | 2.7 | 6 | 6 | Recovered completely |
| 11 | − 6.1 | − 7.2 | −14.2 | — | 0.5 | 8 | 6 | Recovered completely |

### 3. Influence of Temperature on Velocity of Forward Translational Motion

Individual Paramecia were observed continuously as their environing temperature dropped and then ascended, and the forward velocity was measured as frequently as possible by use of an eye-micrometer and a stop-watch (Glaser, '24–'25). The cooling was in each case continued until translational motion was completely halted; then the warming process was immediately commenced. ·

Data were recorded for thirty individuals. These individuals varied so much in their speed of movement at any observed temperature point, as the temperature fell and then rose, that averages are futile. The general result obtained, however, is that the velocity decreases as temperature falls and increases as the temperature rises. Organisms were observed moving translationally at temperatures as low as − 7.4° C.

### 4. Mass Resistance to Low Temperatures

In table I it is noted that some of the individuals exposed to low temperatures died, whereas others survived. Further, in a series of preliminary experiments, of 23 specimens exposed individually to low temperatures 13 succumbed. Such results obviously made desirable an estimation of the quantitative effect of low temperatures on viability. Accordingly, numbers (2–116) of individuals were imprisoned in a series of capillary tubes, by means of the centrifugation technique described above; and these aggregations of organisms were subjected to a gradual reduction of their temperature to a predetermined low point, and were then immediately warmed. The cooling process occupied 5–15 mins., as did the warming process. Approximately half an hour after the low temperature exposure, counts of dead organisms in both the test capillary and a control capillary were made with the aid of a low-power microscope. Then, in order to count the total number of organ-

isms originally imprisoned, those surviving the low-temperature exposure were killed (since they swim about too actively to be counted) by careful application of any hot metal object (*e.g.*, a heated dissecting needle) under low-power microscopic observation. These two counts supplied the data upon which are based the calculations of the percentage of individuals surviving a temperature exposure.

The results obtained are:

TABLE II. *Survival of Paramecium under low temperature*

| | Tests | | | Controls | | |
|---|---|---|---|---|---|---|
| Temp. (° C.) | Indi-viduals Exposed | Number of Tubes Em-ployed | Average Percentage Surviving | Indi-viduals Used | Number of Tubes Em-ployed | Average Percentage Surviving |
| 0 | 77 | 7 | 100.0 | 61 | 4 | 100.0 |
| − 2 | 151 | 7 | 73.5 | 54 | 4 | 98.1 |
| − 4 | 100 | 4 | 93.0 | 132 | 3 | 100.0 |
| − 7 | 232 | 7 | 88.1 | 74 | 3 | 98.6 |
| − 8 | 145 | 7 | 96.5 | 82 | 2 | 98.8 |
| −10 | 113 | 7 | 99.1 | 149 | 4 | 100.0 |
| −12 | 66 | 9 | 98.5 | 11 | 3 | 100.0 |

Taking the results for exposures to a temperature of — 8° C. by way of example, it may be seen that of 145 individuals subjected to this low temperature in 7 separate capillary tubes (an average of 21 organisms exposed together in each of 7 tubes), 96.5 per cent survived. Of the 82 control organisms, incarcerated in 2 capillaries and subjected to treatment identical with that experienced by the 145 test organisms, except that they were maintained at room temperature, 98.8 per cent survived. More than 90 per cent of all organisms survived mass exposures to all low temperature points specified, with the exceptions of — 2° C. and — 7° C.

## DISCUSSION

### 1. Relationships to Previous Investigations

That a liquid enclosed in a capillary tube can be undercooled is a long-known phenomenon (Borovik-Romanova, '24), the present application of which to an aqueous culture medium allows one to expose microscopic forms to sub-zero temperatures and to observe them during such exposure. A serious difficulty enters, however, in that the maximum undercooling obtainable in any given experiment is not predictable, since the factors determining maximum undercooling are largely unknown. As a consequence, one must momentarily expect the undercooled aqueous medium to crystallize and destroy the imprisoned organism(s), particularily if it be cooled below a certain temperature (which in the present experiments with hay infusion was approximately — 10° C.).

The observations herein recorded touch upon the literature of low temperature biological effects at various points. Thus, the observation of Rossbach (cited by Semper, '81, p. 108) to the effect that the ciliary beat of *P. caudatum* ceases at a temperature of $+ 2°$ C. has not been corroborated; rather, cilia of Paramecium have been observed to move during exposure to an environing temperature of $- 14.2°$ C. Again, the morphological degeneration accompanying exposure to low temperature would appear to be much the same phenomenon as that recorded by Greeley ('01–'02) for *Stentor caeruleus;* likewise, the apparent volume increase accompanying this morphological degeneration is in entire accord with the results obtained by Efimoff ('24) and by Payne ('30). However, the writer has not found, as did Efimoff ('24), that Paramecium can survive crystallization of its environing medium. The observations herein recorded indicate that experiments such as those of Glaser ('24–'25), on the effect of temperature on locomotion of Paramecium, may be extended considerably in the direction of low temperatures. Lastly, the simple fact of recovery from an exposure to sub-zero temperatures has previously been demonstrated for a vegetative protozoon only by Efimoff ('24), though it has been shown for various other forms by a number of observers (*e.g.* Rivers, '27; Salvin-Moore and Barratt, '08; Gaylord, '08; Tanner and Williamson, '28; Wright, '27; Lipschutz and Illanes, '29).

## 2. General

That low temperature decreases the rates of metabolic processes in Paramecium appears obvious from the resulting decrease of translational velocity alone. In addition, it appears that deleterious influences supervene, for the marked tendencies toward backward swimming and non-translational spiralling are decidedly abnormal; and, furthermore, the failure of the cell to be propelled through the water, despite the continued beating of the cilia, indicates that the normal ciliary coordination is disrupted by the low temperature. The swelling and disintegration resulting from prolonged, intense exposures may possibly be due to a hydrolytic cleavage of molecules of the protoplasmic constituents, and an accompanying increase of internal osmotic pressure (Bovie, '16). Also, the alteration in optical differentiability of the nucleus which has herein been noted to accompany injury of Paramecium by excessive centrifugation, heat, and low temperature, and by van Herwerden ('30) to appear in epithelial cells as a result of treatment with dilute acetic acid, may likewise be surmised to take its origin in some fundamental alteration of the nucleoplasm. A simple explanation of the uniformly fatal effect of crystallization of the organism's aqueous medium is to the effect that the cellular water concomitantly becomes solidified, thereby initiating a thorough disorganization of the protoplasm.[3] The fact that Paramecia survive short exposures to vari-

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[3] See, however, results of Chambers and Hale ('32) in which internal freezing did not follow upon crystallization of the environing medium, but was induced by introducing an ice crystal into the cells.

ous low temperatures when massed together in a capillary tube (table II), whereas individuals exposed singly in capillaries are very prone to succumb, would indicate a group protection against low temperatures, analogous to the examples of group protection against high temperatures cited by Allee ('31, pp. 217 and 276).

## SUMMARY

1. A simple apparatus is herein described, by use of which Paramecium has been exposed to sub-zero temperatures in a liquid medium and observed microscopically during such exposure.

2. Observations are herein described dealing with the effects of low temperature on (1) ciliary and bodily movements, (2) translational velocity, and (3) viability of the organisms. Also, observations on a few other effects of the low temperature on Paramecium are noted.

3. The observations are reviewed in the light of their relationships to earlier works.

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# SOME RELATIONSHIPS BETWEEN SOIL TYPE AND FOREST SITE QUALITY

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A review of the literature reveals a scarcity of information dealing with the relationship of forest site quality to soil type. This relationship has an important bearing on the economics of land use because of the increased general interest in the reforestation of idle lands. Extensive studies made in Otsego County, New York, during 1933 indicate that a broad but definite relationship exists between different soil types and the different types of humus layer, the amount of windfall, and the rate of survival in forest plantations. Additional observations made in Otsego, Schuyler, and Steuben Counties during 1934 in general substantiate the 1933 studies. If such correlations can be reduced to a practical working basis and combined with an evaluation of climatic factors and the existing flora, a degree of certainty, not now present, can be injected into the reforestation program of any region.

The counties where the correlations to be described were established, are located in east-central and south-central New York. The area ranges in altitude from 1100 to 2300 feet. It is an extension of the Northeastern Appalachian Plateau, and is traversed by well-developed stream valleys. A considerable percentage of the cleared hill land is now idle; some of it has been recently reforested by the New York State Conservation Department. Except for several relatively large tracts of timber owned by estates and institutions, the forest land consists of farm woodlots.

The topography of the areas studied is predominantly rolling, but tracts ranging from flat to rough broken land are included. Neither the degree of slope nor the aspect appears to be of sufficient importance to cause a marked difference in the type of humus layer.

The forest land of the areas studied is characterized by the almost universal presence of hard maple and beech (table II), with varying amounts of other species.

The soils of the areas are derived from glacial deposits. Genetically the soils are young, in that they are strongly influenced by the character of the parent material. The color of the major soil profiles indicates that they are podzolic. The well to moderately drained acid soils are characterized by a slight podzol development; the profiles of the alkaline soils are typical of the brown forest soils. These soils are representative of the Northeastern Appalachian Plateau and the Catskill Region of New York. They are also similar in economic usage.

## SOIL CLASSIFICATION AND APPLICABILITY

The soils of the areas investigated are classified into 19 soil types. It was noted during the progress of the work that the type of humus layer, the amount of windfall, and the rate of survival in plantations were strikingly different on certain soil types but amazingly similar on a number of soil types possessing certain soil characteristics in common. The soil characteristics of greatest importance in the areas studied appear to be lime content of the entire soil profile, degree of drainage, and depth, structure, and consistency of the subsoil. Table I has been constructed to show how soil-survey separations may be correlated and grouped by soil characteristics of greatest importance to the forester.

TABLE I. *Soil types* [1] *grouped by major soil characteristics. The surface texture is uniformly a gravelly silt loam*

Non-limestone soils strongly influenced by non-calcareous gray and red sandstone, acid throughout the profile.

    Deep, poorly drained soils: Chippewa, Norwich, and Holly.

    Deep, imperfectly drained soils: Fremont and Volusia.

    Deep, moderately drained soils: Laurens and Wellsboro.

    Deep, well-drained soils: Wooster, Bath, Otisville, and Chenango.

    Shallow, well-drained soils: Lordstown, Lackawanna, and Culvers.

Limestone soils, alkaline to calcareous subsoils.

    Deep, poorly drained soils: Lyons.

    Deep, well-drained soils: Honeoye and Ontario.

    Shallow, well-drained soils: Farmington.

Organic soils.

    Muck.

A study of table I shows that the entire soil profile is considered in evaluating the factors affecting site quality. The necessity of comparing the entire soil profile is brought out by a comparison of the non-limestone soil groups in figure 1 and table III. The deep, poorly drained soils are characterized by the best type of humus layer, but also by the shallowest rooting and severe windfall damage. No significant difference in texture could be detected between the soil groups, although they varied widely in humus type and in depth of rooting. This finding is contrary to that of Haig ('29), who concludes, from studies made in southern Connecticut, that soil type is but slightly superior to soil class (groupings by surface texture) as a measure of soil fertility.

The placing of several soil types in one group, as in table I, does not necessarily mean that the different soil separations are without significance. For example, the Otisville and Wooster separations are grouped together. The Otisville soils are, however, inherently lower in productivity than the Wooster soils, because their more open, more gravelly subsoils are less retentive of moisture and nutrients. The grouping and evaluation of soil separations in

[1] The classification is tentative, since the final correlation of these soils is still pending.

relation to forest site quality must always be based on a thorough study of the soil-survey bulletin as a guidebook. There are, however, certain separations, especially those based on the color of the parent material, that appear to be of little significance in evaluating forest site quality. For example, the Lordstown, Culvers, and Lackawanna separations are placed together in one group in table I. No consistent difference in type of humus layer, amount of windfall damage, and rate of survival, could be detected between these soil types.

No close correlation was observed between forest tree species and the individual soil types. A study of table II indicates the general prevalence of hard maple and beech, irrespective of soil groups.

TABLE II.  *Order of occurrence of major forest trees by soil groups*  •

| Non-limestone soils | | Limestone soils |
| --- | --- | --- |
| Well drained | Moderately to poorly drained | Well to poorly drained |
| Hard maple (*Acer saccharum*) | Hard maple | Hard maple |
| Beech (*Fagus grandifolia*) | Beech | Beech |
| Hemlock (*Tsuga canadensis*) | Hemlock | White ash (*Fraxinus americana*) |
| White pine (*Pinus strobus*) | White ash | Basswood (*Tilia americana*) |
| Red oak (*Quercus borealis* var. *maxima*) | Basswood | American elm (*Ulmus americana*) |
| Rock oak (*Quercus montana*) | White pine | |
| Yellow birch (*Betula lutea*) | Red maple (*Acer rubrum*) | |

Basswood and white ash occur chiefly on both the limestone soils and the moderately to poorly drained non-limestone soils. The oak-pine type occupies a relatively small acreage on some of the well-drained slopes of the major valleys in the region of the non-limestone till soils.

Another method of measuring the fertility of forest land is the use of plant indicators such as those developed by Heimburger ('34) in an intensive study in the Adirondacks. His numerous tables show a strong correlation between indicator types, colloidal content of the soil, lime content of the $F$ layer, type of humus layer, and richness of the forest type. The poor correlation, however, between the lime content of the mineral horizons taken at irregular depths, and the richness of the forest type, suggests the desirability of comparing the entire soil profile at uniform depths.

Since soil classification does not change as the result of silvicultural treatment and forest succession as do plant indicators, it would seem that the grouping of soil separations by major soil characteristics should form the primary basis for estimating forest site quality. The additional weighing of climatic factors and the existing flora would give silviculturists a more adequate foundation for determining the most suitable forest practice of each area.

Soil characteristics are of great importance in classifying the potential forest-soil productivity of reforestation areas. Plant indicators alone are especially misleading on the non-limestone soils, since the same flora tends

to occur irrespective of the degree of subsoil drainage, sheet erosion, and inherent productivity.   Many coniferous plantations have suffered severe injury from heaving on imperfectly drained areas, whereas little or no such injury has occurred on the well-drained areas.
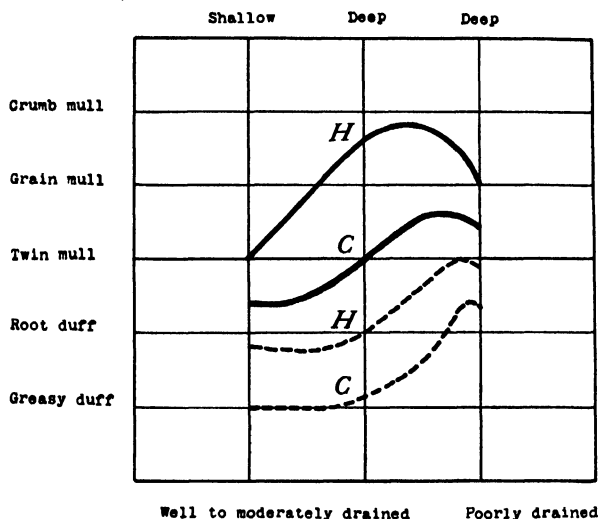


FIG. 1.   Correlation of humus type with degree of drainage, depth of subsoil, lime content, and species. ——— limestone; - - - - non-limestone; *C*, hemlock and white pine; *H*, hard maple, basswood, white ash, and beech.

## INFLUENCE OF SOIL TYPE ON HUMUS DEVELOPMENT

Soil characteristics were found to be more important than forest tree species in the development of the type of humus layer.   A study of figure 1 shows that it is possible to obtain a better type of humus layer under hemlock on limestone till soils than under hardwoods on non-limestone till soils.   The most important soil factor in the development of the humus layer seems to be the lime content.   The best types of humus layer, grain [4] to crumb mull, are found under natural associations of hard maple, basswood, white ash, and beech on the deep, well to moderately drained, limestone till soils.   These soils are alkaline at a depth of about 30 inches, and at that depth frequently contain free carbonates.   In contrast, a root duff was invariably found under the same association of tree species on the deep, well to moderately drained, non-limestone soils which were studied in 1933.   However, a new humus type, " thin detritus mull," was observed on similar soils in 1934 in widely scattered areas in east-central and south-central New York.

Thin detritus mull intergrades in characteristics between root duff and detritus mull, and possesses an intermediate flora.   It tends to occur in areas where the reaction of the subsoil at a depth of 30 to 36 inches ranges from

[4] Nomenclature of Romell and Heiberg ('31).

pH 6.0 to 7.0, whereas root duff occurs where the subsoil is below pH 6.0. Since pH values increase logarithmically, it seems logical that soil separations based on pH 6.0, instead of the present soil-survey separation at pH 7.0, would be more significant in determining the influence of the reaction on humus type. Field observations also indicate that the presence or absence of free carbonates in the soil warrants an additional soil separation.

The poorest type of humus layer, greasy duff, was found under natural associations of hemlock and white pine on the well to moderately drained non-limestone till soils and their steep phases. A twin mull, however, was observed under a pure stand of hemlock on a deep, well-drained, limestone till soil. All other factors being equal, a poorer humus type was observed on all soil types under hemlock, white pine, rock oak, and red oak, than under American elm, hard maple, basswood, white ash, black cherry, *Prunus serotina,* yellow birch, and beech. Natural mixtures of the latter species with the former tend to improve the structure and consistency of the humus layer. This arrangement of forest tree species is in general agreement with the sequence of " soil-improving " value of forest tree species made by Plice ('34), which was weighted on base content, antacid buffering capacity, and acidity of the litter. Alway, Kittredge and Methley ('33) show that on the same soil type, Cass Lake fine sand, the lime content and the nitrogen content, respectively, of the forest floor of the maple-basswood type exceed those of white pine and are much greater than those of jack pine, *Pinus banksiana,* and Norway pine, *Pinus resinosa.* The article does not state whether or not this difference is sufficient to develop a different humus type.

The second major soil factor in the development of the humus layer is the moisture content of the soil, which is affected by the height of the ground-water level and the depth, structure, and consistency of the subsoil. Further inspection of figure 1 indicates that mull is found only on those deep non-limestone soils which are poorly to imperfectly drained. When these soils are moist, the granular structure of the *H* layer tends to be destroyed easily under moderate pressure. The soil characteristic indicating poor drainage is the strongly mottled rusty brown and gray layer which occurs directly underneath the humus layer or within 10 inches of the surface. This condition, which is really a perched water table, is caused by an impermeable, compact or cemented, structureless, strongly mottled layer in the upper subsoil.

A duff is usually found on both the deep and the shallow, well to moderately drained, non-limestone till soils and their steep phases. Such soils are characterized by a deep yellowish brown upper subsoil and by little if any mottling in the lower subsoil. A structureless greasy duff was observed under white pine and hemlock on the non-limestone soils just described. A root duff tends to be formed under hard maple, basswood, beech, and white ash, and also under mixed hardwoods and conifers on similar soils.

The moisture-holding capacity of the soils seems also to be related to the

depth of soil above the bed rock. All other factors being equal, the humus layer tends to possess better structure on the deep, well-drained, till soils than on the shallow till soils influenced by the same parent material. The humus layer of shallow soils tends to become more strongly matted and to possess poorer structure as the depth to bed rock decreases. A somewhat deeper humus layer possessing larger aggregates, was consistently observed on deep limestone till soils having a heavy compact subsoil with a tendency to platy structure, than on similar soils having a gritty, moderately cemented, structureless subsoil.

### INFLUENCE OF SOIL TYPE ON ROOTING

The amount of windfall noted in the forest land which was studied appears to be strongly influenced by the depth and character of the rooting of the forest trees, which is directly affected by the degree of drainage and by the depth, structure, and consistency of the subsoil. The presence of a hummocky or "hog wallow" appearance of the forest floor was taken as an indicator of the amount of windfall.

The relationships between subsoil characteristics and depth of rooting (table III) have been substantiated by studies of more than 300 soil profiles on non-limestone soils in the Arnot Forest. A study of table II shows that very shallow rooting occurs on the poorly drained soils. A marked amount of windfall was noted on these soils.

The structure of the subsoil also appears to exert a profound influence on the depth of rooting. An excavation in a stand of beech, hemlock, and red oak on a deep, moderately drained, non-limestone soil revealed that there was almost no rooting below a depth of 15 inches. Below that depth the subsoil becomes lighter in texture, tightly cemented in place, structureless, and drab gray. There was a marked amount of windfall in the adjacent forest. Similar observations were made on red non-limestone soils of the same soil group. A further study of table III indicates that the deepest root-

TABLE III.    *Relationships between subsoil characteristics and depth of rooting*

| Subsoil characteristics | | | | | Depth of rooting |
|---|---|---|---|---|---|
| Depth | Consistency | Structure | Bed rock | Drainage | |
| Deep | Compact | Structureless | —— | Poorly drained | Very shallow |
| Deep | Compact | Structureless | —— | Imperfectly to moderately drained | Shallow |
| Deep | Compact | Platy | —— | Well-drained | Deep |
| Deep | Firm | Structureless | —— | Well-drained | Deep |
| Shallow | Firm | Structureless | Massive | Well-drained | Shallow |
| Shallow | Firm | Structureless | Thin-bedded | Well-drained    . | Medium |

ing occurs on deep, well-drained soils which have either firm, structureless subsoils or compact subsoils with a platy structure. There was little or no windfall on these soils, except where the woods were adjacent to exposed areas of cleared land.

The structure of the underlying bed rock is of importance in determining the depth of rooting in shallow soils. A considerable amount of windfall was noted on shallow, well-drained soils. Studies of suitable road cuts and quarries revealed massive, continuous layers of sedimenary rock within 3 feet of the surface. There was, however, an appreciable percentage of forest land on the same soil types which was free from windfall. For example, a virgin stand of white pine, hard maple, and black birch, *Betula lenta,* showed little windfall despite the fact that it was located on an exposed west slope of 15 to 20 degrees. Numerous roots were observed following cleavage lines in the underlying thin-bedded gray sandstone.

The occurrence of considerable windfall on the well to moderately drained shallow soils underlain by massive bed rock may also be related to a perched water table immediately above the bed rock. Ground-water studies made by the author on similar soils in the Arnot Forest during 1934 repeatedly showed the presence of free water for many weeks during the spring and fall months. Records obtained from soils underlain by thin-bedded rock strata indicate the absence of a perched water table.

## INFLUENCE OF SOIL TYPE ON SURVIVAL IN PLANTATIONS

The reforestation policies of the Northeast, with few exceptions, have consisted in planting entire tracts with conifers regardless of soil conditions. A study of soil conditions in coniferous plantations revealed excellent survival and good growth on the well to moderately drained soils. In contrast, medium to slow growth and low survival usually occur on the imperfectly to poorly drained soils, especially where the surface water is allowed to accumulate.

Five coniferous plantations have failed in as many years on the same area of a poorly drained soil in Otsego County. The species planted were Scotch pine, *Pinus sylvestris,* in all five years, white pine in the last three years, and a mixture of the preceding species with jack pine, red pine, Norway spruce, *Picea abies,* and red spruce, *P. rubra,* in the last year. A casual examination of such areas, even during periods of drought, reveals a dark gray surface layer which is directly underlain by a layer heavily mottled with rusty brown and gray. It is imperative to determine, before reforesting the areas, where the natural drainage is insufficient. Such areas should not be planted unless adequate drainage is provided.

Numerous areas of low survival were noted in a nine-year-old red pine plantation located on the steep phase of a deep, moderately drained, nonlimestone soil. There was a good correlation between areas of low survival, and seepy spots which were characterized by a dark gray surface soil underlain by a strongly mottled layer.

The partial or complete heaving-out by frost, in plantations of coniferous trees irrespective of species, is serious on poorly to imperfectly drained soils. Ground-water studies made by the author on similar soils in the Arnot Forest

show that a perched water table often exists for long periods during the spring and fall months. The length of time that the perched water table remains appears to depend on the rate of precipitation and the depth to the impermeable, compact, mottled rusty brown and gray layer. In contrast, heaving and the presence of free water have been observed rarely on well-drained soils, even during the wettest periods.

## SUMMARY

A method of grouping and evaluating soil types is here presented, for several major factors influencing forest site quality. The entire soil profile must be considered. Soil types are grouped by soil characteristics of greatest importance in the areas studied. These are: lime content of the entire soil profile; degree of drainage; and depth, structure, and consistency of the subsoil. The principles of this method should form the primary basis for evaluating forest-site quality and the potential forest-soil productivity of reforestation areas.

Certain major soil characteristics as grouped by soil types were found to be more important than tree species, in the development of the type of humus layer. Duff occurs on the better-drained non-limestone soils. Mull is found on the poorly to imperfectly drained soils of similar derivation, and on all limestone soils. All other factors being similar, the well to moderately drained soils possessing superior moisture-holding properties develop the best humus layer. The litter of hemlock, white pine, rock oak, and red oak gives rise to a poorer type of humus layer than does that of American elm, basswood, white ash, hard maple, black cherry, yellow birch, and beech, on the same soil type.

The amount of windfall appears to be strongly influenced by the average depth of forest-tree rooting, which is directly affected by the degree of drainage and the depth, structure, and consistency of the subsoil.

There is a high mortality in coniferous plantings on poorly drained soils. whereas excellent survival occurs on the well to moderately drained soils. Heaving and resultant slow growth in coniferous plantations is serious only on poorly to imperfectly drained soils.

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# REVIEWS

## Biological Forest Types in the Adirondack Region.[1]

It is obvious that the efficient use of land, except for building lots, roads, etc., requires a knowledge of its productive capacity in terms of plant life which may be utilized directly, or converted into animal life. It is also evident that the vegetation growing on a tract of land undisturbed for long periods of time should bear some relation to the productive capacity of the land because it is the result of the total environmental complex. The general bearing of the existing vegetation on the agricultural possibilities of land has long been recognised and used, but the detailed analysis of vegetation for purposes of classifying land is of more recent development and involves many intricate problems. The need for using vegetation as a guide to the quality of the land has been greatest in forestry because it is impracticable to use the methods suitable for cultivated lands.

Foresters in America base their descriptions and classifications of forests for purposes of management on the composition of the stand (the "cover type"), e.g., the spruce type, the long-leaf pine type, etc., or on topography (the "physiographic type"), e.g., the ridge type, the slope type, etc., or sometimes on a combination of both, as the spruce slope type. The site quality, or productive capacity, or any given type is based on the height attained at a given age, usually 50 years.

Cajander,[2] in Finland, conceived the idea of biological types, in which the ground vegetation, because it is the result of the interaction of the environmental factors, should be taken as an indicator of the productive capacity of the land. Accordingly he worked out his now well-known system of forest types which is used throughout Finland. In Sweden, though Cajander's actual types are not considered applicable, the designation of types is also by the ground vegetation. In Cajander's types, the composition of the forest is not always the same for any given type. Thus for example the *Myrtillus* type includes stands of both pine and of spruce, each with a rate of growth determined by the complex of factors indicated by the presence of *Myrtillus*. The reviewer has long hoped that someone would try Cajander's biological types in America. In 1929 Ilvessalo,[3] who has worked with Cajander, made a preliminary test and found the system applicable to the

[1] Heimburger, Carl C. 1934. Forest-type studies in the Adirondack region. *Cornell Univ. Agr. Exp. Sta., Mem. 165,* 122 pp., 14 figs. *Ithaca, N. Y.*

[2] Cajander, A. K. 1909. Über Waldtypen. *Acta Forest. Fennica* **1**: 1–175.
——. 1926. The theory of forest types. *Acta Forest. Fennica* **29**(3): 1–108.

[3] Ilvessalo, Y. 1929. Notes on some forest (site) types in North America. *Acta Forest. Fennica* **34**(39): 1–111.

relatively simple lodgepole pine forests, and probably also to others. But Heimburger's is the first attempt at a comprehensive application of biological types to a forest region in America. Of course it must be remembered that the forests of the United States are vastly more varied and complicated than those of Finland, even aside from the question of area covered. The Scandinavian forests are mostly of pure pine, *Pinus sylvestris,* or spruce, *Picea excelsa,* or mixture of both, with varying amounts of birch throughout, and are relatively uniform and free of undergrowth.

The Adirondack region affords an exceptional opportunity for a study of forest types because of the large amount of virgin forest in the 2,000,000 or so acres of the Adirondack State preserve. The work was not, however, confined to the State preserve, but included also some second growth and some lightly culled forests, and extended into the White Mountains of New Hampshire, and the Laurentian Mountains in Canada. On the other hand, the Adirondack region has disadvantages in the variety and complexity of its forests, as compared with more uniform forests like lodgepole pine. Also a virgin forest presents difficulties in measuring the rate of growth and volume production which serves as a criterion of the productive capacity of the different types.

Heimburger's work was done inductively, so that the types should force themselves upon the observer instead of being deduced from predetermined principles. The region was divided into three floristic provinces; the subalpine, comprising the upper forested slopes of the mountains, the western, including the major part of the region, and the eastern, representing the valleys in the eastern part of the region.

The ground vegetation was analysed on a large number of plots by the Raunkiaer method as used by Bornebusch,[4] and the detailed results are presented in a series of tables, as well as graphically in charts. The soil on each plot was studied intensively, and tables are given showing for each plot the depth and type of humus layer (based on Romell and Heiberg's classification [5]) divided into Hesselman's $F$ and $H$ layers,[6] and the nitrifying power of each of these layers, the pH, lime content, and loss on ignition; for the mineral soil he presents the texture, the lime content, and data on profile and site. There is also a table showing for each plot the location, elevation, and composition of the main stand. The text descriptions are thus supported by field and laboratory data, enabling anyone to draw his own conclusions as to the basis on which the types have been recognized. The whole represents an enormous amount of detailed work.

[4] **Bornebusch, C. H.** 1923–25. Skovbundsstudier I–III; IV–IX (Disquisitions on flora and soil of Danish woodlands). *Det forst. Forstogsvaesen i 'Danmark* **8:** 1–148, 181–288.

[5] **Romell, L. G., and S. O. Heiberg.** 1931. Types of humus layer in the forests of Northeastern United States. *Ecology* **12:** 567–608.

[6] The $F$ layer is the layer in which decomposition is going on, the structure still being visible, the $H$ layer is the amorphous humus.

The soil tests showed nitrifying power in the humus layers of the richer types, but practically none in those from the poorer types. The humus of the richer types had a higher lime content than that of the poorer types; but the mineral soil showed practically no correlation between lime content and productivity of the types. The reaction of the humus was very acid in some of the richer types, and showed little relation to productivity.

The types depend on climate, geological formation, topography and drainage. The composition of the main stand is not always the same on any one type, nor is the type the same for any given composition of the main stand. Differences in composition of the main stand in a type which occurs in more than one region are attributed to climate.

The author recognises 22 types: 3 in the subalpine series; 9 in the western series, of which 6 are softwood (coniferous) and mixed-wood types and 3 hardwood types, and 10 in the eastern series, of which 5 are softwood and mixed-wood and 5 hardwood. This is rather a large number; some of the types are based on too few plots, and some are of limited distribution and minor importance. Further work, and the application of the types in the field, will doubtless result in improvements and probably in simplification and in reduction of the number of types.

The growth data are unavoidably inadequate, but the diameter growth of dominant red spruce, *Picea rubra,* on 5 types shows an increase in rate from the poorer to the richer types.

In general, the types correspond well with the tree species and development of the stand in the forests of the region. In the western series the *Cornus-Maianthemum* type (Co-Ma T) indicates land suitable for pine. When Hesselman visited America in 1927 he noticed the *Cornus* in one of the New Hampshire forests, and remarked that the land was good for conifers. The *Oxalis-Cornus* type (O Co T) is the best for red spruce. The *Viburnum-Oxalis* type (Vi O T), which occupies the largest area in the Adirondacks, is more productive than the preceding type, and, although containing spruce in mixture, allows so much competition from the hardwoods that it is unsuitable for growing future crops of spruce.

The more important types described by Heimburger are probably applicable throughout the northeastern forests, that is, Hawley's [7] spruce region, which includes, besides the Adirondack Mountains, most of Vermont, New Hampshire and Maine, as well as the provinces of Quebec, New Brunswick and Nova Scotia in Canada. The *Cornus-Maianthemum* type and *Viburnum-Oxalis* type cover large areas in Maine and the White Mountains, and some of the other types can also be found there.

Applying Heimburger's types to Mt. Desert Island, Maine, which is remarkable for the large number of distinct types it contains, the type covering the largest area, described by Moore and Taylor [8] as the mixed conifer, cor-

[7] **Hawley, R. C.** 1912. Forestry in New England. *Wiley & Sons, New York.*

[8] **Moore, Barrington and Norman Taylor.** 1927. Vegetation of Mount Desert Island, Maine, and its environment. *Brooklyn Botanic Garden Memoirs* **3**: 1–151.

responds with Heimburger's *Cornus-Maianthemum* type. Parts of the spruce type correspond with the *Hylocomium* type, only *Hypnum schreberi*, which Heimburger speaks of as abundant, is here dominant. Mount Desert Island contains also a small but well developed example of the *Viburnum-Oxalis* type, described by Moore and Taylor as northern hardwoods-spruce. In places it is possible to find examples of Heimburger's *Vaccinium-Myrica* type and *Cornus-Pyrola* type. Some of the other Mt. Desert types belong south of the region covered by Heimburger.

Enough has been said to show that Cajander's system of biological types can be applied in American forests, but they require a high degree of ecological and forestry training, combined with endless patience and perseverance, to work out. Probably each major forest region will require its own set of types. So the application of biological types in American forests will be slow, but it is hoped that it will eventually be made. Once the types have been worked out, their application in the field is not difficult. It is necessary to know something of the changes caused by cutting and burning, so as to be able to recognize a type which has undergone these changes. However, most foresters are familiar with cut-over and burned lands, and the successional trends going on.

Cajander's biological types represent applied ecology yielding results of great practical value. In this particular study Heimburger has given a much needed guide for deciding the troublesome question as to lands on which it is worth while trying to maintain spruce in mixture with the hardwoods, and those on which the competition of the hardwoods will make the attempt a waste of money and effort. A chart in which the types he has recognized are arranged according to Sukatschew's [9] system shows this plainly.

One might criticize the use of the rod as a unit of measure in speaking of Raunkiaer's method, and the lack of a summary, but these are minor matters in such an important contribution to forest ecology.

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## ROLE OF FIRE IN PASTURE MANAGEMENT [1]

The practice of burning grass is an old one. It was extensively used by the Indians to attract game animals in early spring and to facilitate hunting. It is also highly probable that a large portion of the prairie was burned periodically during very dry years from natural causes.

Burning of bluestem pastures is a practice that is generally followed in eastern Kansas and particularly in the Flint Hill region. This great area

[9] **Sukatschew, W. N.** 1932. Die Untersuchung der Waldtypen des osteuropäischen Flachlandes. *Abderhalden's Handb. Biol. Arbeitsmeth.* 11(6): 191–250.

[1] **Aldous, A. E.** 1934. Effect of burning on Kansas bluestem pastures. *Kans. Agr. Exp. Sta. Tech. Bull.* 38: 1–65. 12 figs.

occupies about three million acres of pasture land extending north and south across the western part of the eastern one-third of the state. It is contended that unless the dead grass remaining from the previous year's grazing is burned it will result in irregular grazing, *i.e.*, the rocky slopes will be undergrazed and the ridge tops overgrazed. Burning is also believed to promote earlier growth in spring; it destroys the dead, unpalatable grass and permits the new growth to be grazed to better advantage. It is also believed to be effective in controlling weeds. Conversely, many persons have considered burning a harmful practice since fire is usually associated with destruction. They believe there is some loss in fertility of soil as well as a decrease in the density and vigor of the desirable pasture plants.

Preliminary studies [2] on the effect of burning showed a slight decrease in the yield but an increase in the population of grasses. Since there was little difference in the vegetation of the burned and unburned areas, the conclusion was reached that burning had not been injurious.

In 1926–27 experiments were started to determine the effect of burning on (1) the yield, (2) control of weeds and brush, (3) quality of vegetation, (4) soil moisture and soil temperature, (5) composition and succession of the vegetation, (6) starting growth in spring, and (7) effect upon fertility of the soil. The experiments were conducted on two areas of bluestem pastures near Manhattan, Kansas, under a mean annual precipitation of 31.5 inches, about three-fourths of which falls during the growing season. The soil in the Casement pasture area is nontillable both because of limestone outcroppings and the presence of loose, cherty rock, which also covers the surface. The Derby silt loam of the college pasture, although deep, fertile, and arable, has never been broken.

*Andropogon furcatus* and *A. scoparius* are the dominant grasses of both areas. They are about equally divided in the Casement pasture, and *A. scoparius* comprises about one-half of the entire vegetation in the college pasture. Other important grasses in the two areas include *Sorghastrum nutans, Bouteloua curtipendula, Koeleria cristata, Sporobolus heterolepis, Poa pratensis,* and *Panicum virgatum.* In addition there are numerous subdominant forbs.

The experimental plots (each 33 × 66 feet or larger) were burned annually either in the late fall (December 1), early spring (March 20), medium spring (April 10), or late spring (May 5). Other areas were burned on alternate years. Each burned area contained an unburned check plot. Yields from at least one-half square rod samples of mature vegetation were obtained by clipping in early October.

Burning decreased the yield of the mature vegetation, and the yield was least on the plots burned late in the fall. The plot burned in early spring ranked second, and was followed by the plot burned in medium spring. Plots burned in late spring most nearly approached the yield of unburned

[2] Hensel, R. L. 1923. Effect of burning. on vegetation of Kansas pastures. *Jour. Agr. Res.* **23**: 631–647.

plots. The yield of the unburned plots (college pasture) over a period of six years averaged approximately 48 per cent more than that of the plot burned in the late spring, and 88 per cent more than the plot burned in the late fall. Yield of plots burned on alternate years was greater than that of plots burned annually, varying from 16 to 48 per cent greater, depending upon the time of burning.

Burning had little effect in controlling weeds (forbs) or *Rhus glabra* and *Symphoricarpos* unless it was done very late in spring after growth had begun and food reserves were low. It was not an effective means of eradicating sumach since the minimum point in food reserves does not occur until about June 7. The dominant grasses on the burned plots were more leafy during the early part of the growing season than on the unburned ones. The nutritive content of the forage depended upon the amount of growth. Thus in early June protein content was highest for the vegetation obtained on the plots burned in the late spring, while the older vegetation from the fall- and early spring-burned plots had the lowest protein content.

Water content of soil on the unburned plots was higher than that of any of the burned ones. A thorough analysis of a large number of meter quadrats charted three or four times annually showed that the plant population was greatest on plots burned in late fall and least on those burned in late spring. Plots burned in late fall and early spring had a greater number of plants than the unburned plots. The greater plant population of the late fall-burned plots resulted mainly from an increase in the number of plants (stems) of *Andropogon scoparius*. While late burning in fall caused a successional trend in favor of the little bluestem, in plots burned in late spring the change was toward the coarser grasses, mainly *Andropogon furcatus*. *Poa pratensis* increased on all the unburned plots and was either decreased or eliminated in all the burned ones.

Burning stimulated early growth in spring, owing mainly to the higher soil temperatures. The mean maximum weekly temperatures at a depth of one inch in spring were 10.5° F. higher on the burned plots. Plots burned in late fall or early spring produced a greater growth of vegetation until early in June, after which moisture rather than temperature became the controlling factor in growth. During a five-year period burning caused no measurable decrease either in organic matter or total nitrogen. Accumulation of both these materials in prairie is governed more by root development than by the accumulation of surface materials.

"A properly managed bluestem pasture should be stocked according to its grazing capacity in an average year." Excess forage production may be cut for hay on very favorable years. If this is not feasible, accumulated materials on steeper slopes and other undergrazed parts of the pasture should be removed by burning. "Burning seems to be highly desirable if not essential on bluestem pastures about every other year if they are stocked about the same each year." It may be effectively used in making the utilization of

the forage possible in the less accessible places, but only those parts of the pasture with much accumulated debris should be burned.

In the experiments the burning was always done when the soil was moist, otherwise there might have been excessive burning of the soil and crowns of the plants and distinct injury to the vegetation. Accordingly the results might have been different.

This carefully planned and well executed research, extending over a period of years, adds much to an understanding of the ecology of the prairie in addition to furnishing a scientific basis for the use of fire in improving the range.

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### DISSOLVED OXYGEN AS AN ECOLOGICAL FACTOR IN LAKES [1]

Volume IV of the Thienemann series of brochures relating to inland waters deals with their dissolved oxygen content from a quantitative chemical standpoint, but the present volume considers the oxygen supply of oligotrophic and eutrophic lakes from an ecological point of view. The author points out that a clear knowledge of the oxygen economy of the water is the ultimate aim of a chemical investigation. The general problem of the oxygen supply involves the exchanges between the air and the water and also a study of the production and consumption of this gas within the body of water. In the distribution of the oxygen diffusion plays only a very minor part; the chief factors are the overturning and circulation of the water of the deeper lakes in spring and fall.

The quantity of oxygen serves as an index of the eutrophization of a lake and it depends upon the relation between the various oxygen consuming processes and the volume of the hypolimnion. Respiration, decomposition and absorption by the bottom deposits in the deeper water are the chief factors involved in the consumption of oxygen in the hypolimnion. The rapidity with which oxygen disappears in the process of decomposition indicates the rate at which mineralization of the organic substances returns to the elemental food status, and this shows the intensity of the cycle of matter in the lake.

The importance of oxygen as an environmental factor is discussed in some detail. The scarcity or abundance in a biocoenose determines the abundance and the character of the biota. The relationships between the dissolved oxygen and the other physical, chemical and biological factors are represented by mathematical formulae and by diagrams in several instances.

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[1] Grote, August. 1934. Der Sauerstoffhaushalt der Seen. *Thienemann's Die Binnengewässer* 14: vii + 217 pp. 35 figs. *Stuttgart.*

## ANTHROPO-ECOLOGY OF CHINA [1]

In this book a notably successful attempt is made to relate the development of a people to the factors of the environment, both physical and human. Six general chapters on geography, topography, climate, agriculture, natural resources and relations with other peoples, are followed by 15 chapters of detailed descriptions of the several physiographic regions of the country, The Manchurian Plain, The Southeastern Coast, The Tibetan Borderland, etc. A bibliography, arranged by chapters, occupies 29 pages.

China may be divided into two great ecological regions, the north and the south. The north, with relatively low and uncertain precipitation, has a 4- to 6-month growing season, while in some parts of the south the growing season may extend throughout the year. It is only in the south that rice is the dominant crop, the northern agriculture being based on kaoliang, millet, wheat and beans. In northern Manchuria timber is an important crop. The north is the region of frequent famines. In the north the race is essentially uniform and there is but one prevailing dialect (Mandarin); in the south there is a great mixture of races, including non-Chinese primitive tribes, and a great diversity of dialects.

The author emphasizes the fact that although six-sevenths of the population are concentrated in one-third of the area, cultivation has practically reached the economic limit and, except in portions of Manchuria, the opportunities for bringing new land under cultivations are very few. This situation is due largely to the fact that a great part of the country is predominatingly mountainous. Conceding that crop yields may be slightly raised by improved agricultural practice, still it seems to the author inevitable that before China can enjoy increased material prosperity the birth-rate must be lowered. "This situation was . . . realized by Dr. Sun Yat-sen [as long ago as] 1894 . . ." (p. 23). The people of China, with the physical environment, are likened to a botanic climax formation, "an old stabilized civilization which utilizes the resources of nature to the limit" (p. 3).

Protected by natural barriers, to which the people added the famous Great Wall, China has for many centuries developed under conditions of relative isolation. This development has resulted in the production of a culture rather than a nation as we usually understand the latter term. Politically, the boundaries of China and of the several provinces and outlying territories have experienced many changes in the course of the country's 30-odd centuries of known history, and have sometimes been exceedingly poorly defined.

"The origin of the Chinese people and their culture is obscure," but there is a possibility that they developed right where they are now found (p. 3). Invasions from the west and northwest have been frequent, the characteristic result being assimilation of the newcomers by the Chinese. It appears that

[1] **Cressey, George Babcock.** 1934. China's Geographic Foundations. xvii + 436 pp., 197 fig., map, 36 tables. *McGraw-Hill Book Company, Inc., New York and London.* $4.00.

the North China Plain (lower basin of the Hwang River, etc.) has time and time again received vigorous migrants from the north, probably often as a result of unusually deficient rainfall in arid central Asia, with a subsequent movement to the south of the more ambitious individuals, corresponding somewhat to the westward movement in the United States and Canada.

The author expresses doubt that Manchuria is destined to be colonized to any large extent by the Japanese, who " are distinctly a warm-weather people." An estimate of the future of the country is given in the following words: " All geographic signs would seem to point to China as the ultimate political, industrial, and cultural power in the Orient. When that day of leadership comes, it will be most unfortunate if any of her neighbors are found trespassing " (pp. 217–218).

In preparation for this sympathetic and scholarly work, the author traveled extensively in China, covering 30,000 miles in 6 years. Formerly on the faculty of the University of Shanghai, he is now head of the Department of Geology and Geography at Syracuse University, New York. We need more treatises of this character and quality.

<div align="right">FERDINAND W. HAASIS</div>

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<div align="center">THE STRUGGLE FOR EXISTENCE [1]</div>

This volume should stimulate any ecologist who is interested in the study of populations. A preface to the volume is written by Raymond Pearl to whose school the author may be said to belong, inasmuch as he is a protege of Professor W. W. Alpatov, a former student of Dr. Pearl. There are six chapters covering 160 pages.

Chapter I, entitled " The Problem," reviews the history of the work on the struggle for existence, beginning with Darwin and carrying it through the days of mathematics represented by Sir Ronald Ross's work on the malarial equation and the later work of Lotka and Volterra.

Chapter II is entitled " The Struggle for Existence in Natural Conditions " and is a review of literature, particularly that containing quantitative data on populations of organisms, both plant and animal.

Chapter III is entitled " The Struggle for Existence from the Point of View of the Mathematicians." To one not versed in mathematics, it appears to be admirably handled. He has expressed his equations not only in symbols but also in phrases. He reviews the work of Ronald Ross on malarial incidence and then takes up the Verhulst-Pearl logistic curve at which some of his contemporaries are inclined to look askance. The author makes the interesting statement that while the logistic curve may be too simple a statement of the trend of a population, it often happens in the early stages of re-

[1] Gause, G. F. 1934. The Struggle for Existence. 160 pp. *Williams and Wilkins Company, Baltimore.*

search that a simplified statement does more to aid future progress than a statement that might later be made which would involve too much detail to make it possible to analyze the problem. His statement would seem to find some justification in such fields as genetics where the early simple statements stimulated research although later there were many exceptions found. The chapter proceeds to review the work of Lotka and Volterra as a basis for the presentation of experimental data in later chapters.

Chapter IV, entitled " On the Mechanism of Competition in Yeast Cells," begins the presentation of quantitative data largely based upon the work of the author. Experimental results are compared with mathematical formulae and curves.

Chapter V is entitled " Competition for Common Food in Protozoa " and here he outlines experiments with pure and mixed populations of *Paramecium* and other Protozoa.

Chapter VI treats of " The Destruction of One Species by Another" and is based upon experimental data with *Paramecium caudatum* and *Didinium nasutum*. In discussing his data from various types of controlled cultures the author concludes that when the microcosm approaches the natural condition and contains variable refuges in which the prey may escape the predator, the struggle for existence begins to be controlled by such a multiplicity of causes that he is unable to predict the course of development of each individual microcosm. He states that it is necessary to pass from the language of rational differential equations to the language of probabilities, and he feels that there is no doubt that the corresponding mathematical theory of the struggle for existence will be developed in the language of probabilities. From the study of his data on *Paramecium* and *Didinium* he believes that periodic oscillations in the numbers of the predators and of the prey are not a property of the predator-prey interaction itself as assumed by Lotka and Volterra, but apparently occur as a result of constant interferences from without in the development of the interaction. He believes this is characteristic of populations generally, rather than of his special case. He believes that what he terms an " epidemic " of predators cannot break out until the prey has reached a certain threshold value. Then oscillations begin, which he classes as " relaxation oscillations " as distinct from the " classical oscillations " of the mathematicians. He believes that this type of relaxation oscillation is the one which ordinarily prevails under natural conditions, the so-called classical oscillations existing only under certain special and simplified conditions.

This stimulating volume contemporary with the symposium on quantitative biology from the Cold Spring Harbor Laboratory is a valuable contribution to our literature on the ecology of populations.

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## A University Forest

No type of out-of-door laboratory is likely to prove more useful to future university studies than the forest and especially the forest devoted to experimental ecology and its application as silviculture.

In a recent bulletin [1] such a forest connected with Duke University, Durham, North Carolina, is described. It consists of some 4500 acres in the central portion of the state near the eastern edge of the piedmont plateau. The eastern edge of the forest borders on the university campus. Within its boundaries are represented some fifteen of the forest types characteristic of the piedmont. These range from pure stands of pine through mixed pine-hardwoods to various upland oak types and bottom land forests of gum, birch, and sycamore. Most of the pine stands are even-aged, young to middle-aged, while the hardwoods range from uneven-aged mature or over-mature to second growth woodlands. The entire forest is a state game refuge and certain parts of it, which are open for controlled recreational use, include several picnic sites properly equipped. It is thought that familiarity with the forest and its objectives is likely to promote public appreciation of forest values.

In preparation for its experimental use careful maps have been made showing the extent of the various areas and the compartments and subdivisions which are necessary for complete records. A detailed analysis of each stand has been made for future reference. The maps form a part of the bulletin in which the management policy is outlined. Three principal objectives are emphasized: an example of scientifically managed forest properties for the use of timberland owners in the region; an area devoted to the investigation and solution of forestry problems; and a laboratory for a university school of forestry.

This bulletin is to be followed by others which will present the results of forestry and ecological research in the Duke Forest and elsewhere. These will be awaited with interest.

Geo. D. Fuller

The University of Chicago

## Changes in Tree Trunks

The commonly accepted idea that tree trunks are subject only to yearly increases in diameter seems true in a general way but is subject to certain modifications. With the invention and application of such instruments of precision as the MacDougal dendrograph not only can the rate of growth be measured more accurately but it is also possible to detect daily variations in

[1] **Korstian, Clarence F. and William Maughan.** 1935. The Duke Forest; a demonstration and research laboratory. *Duke University Forst. Bull. no. 1.* 74 pp. 4 maps.

trunk diameter. According to Haasis [1] these consist in diurnal shrinkages and nocturnal swellings amounting to 1.6 mm. These variations occur mostly in clear weather and are very similar for practically all gymnosperms, monocotyledons, and dicotyledons of tree habit. A notable exception seems to be the stems of arborescent cacti.

The shrinkages seem to be due largely to water deficiency however caused. The fluctuations in water content are confined mostly to the peripheral layers of the trunks and sometimes to the thick bark.

Haasis' investigations have resulted in an abundance of detailed data that are presented in tables and graphs. The material includes many tree species from the Pacific coast region. The details of the variations are carefully discussed and are referred to various environmental factors that affect the water supply. An extensive bibliography is appended to the report.

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[1] **Haasis, Ferdinand W.** 1934. Diametral changes in tree trunks. *Carn. Inst. Wash. Publ. 450.* 103 pp.

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# NOTES AND COMMENT

## INTERNATIONAL PRESERVATION OF NATURE

In 1913 an International Conference for the Protection of Nature was held at Bern. Movement was interrupted by the war but in 1925 a Dutch committee was formed, and in 1926 a Belgian committee was organized which, together with other organizations, were combined into the International Office for the Protection of Nature. They issued a pamphlet from Brussels, January 1931, showing photographs of ruthless destruction of animal life in Africa. The introductory paragraphs of this read as follows:

" The protection of nature has in the course of the last years become increasingly important to all lovers of natural beauty, and to those, aware of the richness and abundance of the animal and vegetable kingdoms."

" Today, in modern society every cultivated person watches with dismay the rapid decrease and disappearance of certain vegetation, fauna and picturesque scenery, which add so much to the beauty of this world and at the same time offer to science an incomparable field of investigation."

" If we do not wish solely to bequeath to future generations a mechanical and industrial world, we must take immediate steps to avert this ever increasing danger."

" Added to this, since half a century, colonial powers, rapidly developing new countries, have not given sufficient attention to the danger of inflicting irreparable damage to the scenery, wild life and vegetation of these countries. It must not be thought that these are exaggerated statements which only apply to small areas or to densely populated regions. Blind destruction always preceeds the building up of a prosperous and constructive civilization. Some of the colonies which formerly comprised 92 per cent rich forest land, today do not possess more than 5 to 10 per cent."

At that time the Belgian government had not officially indorsed the movement. Under the date of February 8, the Secretary of the International office at Brussels, Dr. Graim issued the following statement with the request that it be published in Ecology.

" The Belgian Government has by Royal Decree officially recognized the International Office for the Protection of Nature and has appointed the following delegates to be its representatives to the General Council of the Office:

Delegates for Belgium: *Baron E. de Cartier de Marchienne,* Belgian Ambassador in London, and *Count Henry Carton de Wiart,* former Prime Minister;

Delegates for the Belgian Congo and the Mandated Territory of Ruanda-Urundi: *P. Charles,* Minister of Colonies, and *Professor Dr. V. Van Straelen,* Director of the Royal Belgian Museum of Natural History and President of the Institute for National Parks in the Belgian Congo."

The International Office for the Protection of Nature is supported by contributions from the Dutch Government, the " Fondation Universitaire " in Belgium, various committees and societies interested in such work, and a few private individuals. In this country an annual contribution has been made by the American Committee for International Wild Life Protection. This year marks the fifth anniversary of the founding of the American Committee. This committee is made up of representatives of the leading Museums, Zoological Societies, and Sportsmens Organizations that are interested in wild life protection outside of the United States, and includes on its Executive Board Dr. John C. Phillips, Dr. Thomas Barbour, Mr. Charles M. B. Cadwalader, Mr. Kermit Roosevelt, Mr. Arthur S. Vernay, Dr. Alexander Wetmore, and Mr. Harold J. Coolidge, Jr., Secretary. The International Office at Brussels is in need of contributions for the

support of its many activities. Anyone interested should write to the secretary of the American Committee for International Wild Life Protection, Cambridge, Massachusetts.

V. E. SHELFORD

UNIVERSITY OF ILLINOIS,
APRIL, 1935.

### NOTE ON IRON ANALYSES OF ATLANTIC COASTAL WATERS [1]

The possible importance of iron as an accessory substance to marine plant production has been emphasized particularly by Gran [2] but with the exception of scattered observations there has been little attempt at a systematic study of its distribution in the sea. In the absence of published iron analyses for the Atlantic coastal waters of North America these few observations from the Gulf of Maine are, perhaps, of interest in illustrating the possible order of magnitude of the occurrence of iron in the locality.

The water samples were collected with Nansen water bottles by M/S " Atlantis "; three stations (1865, 1880, 1897) in December 1933 and two (2253, 2257) in August 1934. The water was kept unfiltered in ordinary citrate bottles about two weeks before analyses. Iron was determined on the unfiltered sample according to the procedure outlined by Thompson, et al. [3] except that Riedel-de Haën standardized ferricitrate was used in preparing the standard solutions rather than ferrous ammonium sulphate; standard solutions were graduated in intervals of 0.005 mg. Fe per liter. Thus, the results in table 1 represent the quantity of iron per unit volume of sea water sampled by the water bottle, which is not only iron dissolved in sea water (in soluble organic compounds, etc.) but also that which is contained in the bodies of organisms trapped by the water bottle.

The observed range of iron for both seasons, between surface and 340 meters, was 0 to 0.05 mg. Fe per liter but results are insufficient for any conclusions. To gain a true picture of the seasonal variation of iron it appears necessary to consider the nature of the plankton present at the time of observation and to use appropriate filters of pore size sufficient to completely remove from the sample, immediately after collection, all organisms trapped by the water bottle; variations in the quantity of trapped organisms may be sufficient to produce a decided variation in the results.

On the whole the magnitude of results for the Gulf of Maine are within the range of iron values reported for other marine areas. Braarud and Klem [4] found 0.004 to 0.023 mg. Fe per liter for Norwegian coastal waters and Harvey [5] found 0.003 to 0.006 mg. Fe per liter for the English Channel; Wattenberg [6] reported an average value of 0.06 mg. Fe per liter for the tropical Atlantic but considers the value too high. The values in the upper 50 meter stratum of the Gulf of Maine (0.0–0.050 mg. Fe/1) are, in general, slightly lower than those obtained from a surface stratum of similar thickness in Puget Sound (0.030–0.050 mg. Fe/1; Thompson, et al.) while the deeper water of the Gulf of Maine shows values (0.005–0.40 mg. Fe/1) about one-tenth of those recorded for similar depths in Puget Sound.

[1] Contribution No. 63 from the Woods Hole Oceanographic Institution.

[2] Gran, H. H. 1932. Phytoplankton. Methods and problems. *Jour. du Conseil* 7(3): 343–358.

[3] Thompson, T. G., Raymond W. Brenner and I. M. Jamieson. 1932. Occurrence and determination of iron in sea water. *Ind. & Eng. Chem. Analytical edition* 4(3): 288–290.

[4] Braarud, Trygve, and Alf, Klem. 1931. Hydrographical and chemical investigations in the coastal waters off Møre and in the Romsdalsfjord. *Hvaldrådets Skrifter. Nr. 1.* 88 pp. *Oslo.*

[5] Harvey, H. W. 1925. Oxidation in sea water. *Jour. Mar. Biol. Assoc.* 13: 953–969.

[6] Wattenberg, H. 1927. Die Deutsche Atlantische Expedition auf " Meteor." 4. *Bericht. Zeitschr. Gesell. für Erdkunde* nr. 5–6, p. 308.

TABLE I. *Results of the analyses of Atlantic coastal waters*

| Station | Depth in m. | Temperature C. | Salinity 0/00 | Fe mg. per liter |
|---|---|---|---|---|
| 1865 | 1 | 7.10 | 32.81 | .010 |
| December 1933 | 18 | 7.13 | 32.82 | .012 |
| | 37 | 7.14 | 32.86 | .012 |
| Latitude    Longitude | 57 | 7.15 | 32.78 | .012 |
| 42° 39′ N    69° 47′ W | 77 | 7.12 | 32.83 | .020 |
| | 97 | 6.29 | 33.04 | .015 |
| | 121 | 6.06 | 33.25 | .035 |
| | 146 | 6.09 | 33.60 | — |
| | 195 | 6.48 | 34.06 | .033 |
| | 230 | 6.62 | 34.23 | .020 |
| 1880 | 1 | 7.12 | 33.06 | .040 |
| December 1933 | 10 | 7.14 | 33.05 | — |
| 42° 45′ N    68° 48′ W | 19 | 7.13 | 33.27 | .050 |
| | 29 | 7.15 | 33.07 | .038 |
| | 39 | 7.14 | 33.07 | — |
| | 48 | 7.15 | 33.06 | .038 |
| | 58 | 7.14 | 33.07 | .038 |
| | 77 | 7.15 | 33.13 | .040 |
| | 97 | 7.85 | 33.56 | .035 |
| | 145 | 6.75 | 33.92 | — |
| | 172 | 6.63 | 33.87 | .030 |
| 1897 | 1 | 7.04 | 32.51 | .016 |
| December 1933 | 10 | 7.04 | 32.50 | — |
| 42° 25′ N    67° 06′ W | 20 | 7.03 | 32.51 | — |
| | 30 | 7.22 | 32.63 | — |
| | 40 | 7.29 | 32.67 | — |
| | 50 | 7.27 | 32.74 | .010 |
| | 60 | 7.22 | 32.76 | — |
| | 80 | 7.48 | 32.97 | .015 |
| | 100 | 8.06 | 33.58 | .015 |
| | 150 | 8.15 | 34.53 | .015 |
| | 200 | 6.99 | 34.95 | .015 |
| | 250 | 6.78 | 34.98 | .010 |
| | 300 | 6.16 | 34.94 | .020 |
| | 340 | 6.17 | 34.96 | .015 |
| 2253 | 1 | 17.26 | 32.24 | .005 |
| August 1934 | 20 | 14.93 | 32.48 | .025 |
| 42° 25′ N    67° 11′ W | 50 | 8.24 | 32.81 | .005 |
| | 80 | 6.14 | 33.37 | .030 |
| | 99 | 5.31 | 33.72 | .020 |
| | 193 | 7.85 | 34.94 | .025 |
| | 242 | 7.65 | 34.96 | .030 |
| | 292 | 7.16 | 34.93 | .025 |
| | 340 | 6.91 | 34.93 | .025 |
| 2257 | 1 | — | 32.19 | .000 |
| August 1934 | 20 | 16.03 | 32.21 | .000 |
| 42° 26′ N    68° 48.5′ W | 40 | 5.80 | 32.59 | .000 |
| | 50 | 4.80 | 32.66 | .006 |
| | 80 | 3.59 | 32.89 | .004 |
| | 100 | 3.49 | 33.01 | .007 |
| | 120 | 3.70 | 33.13 | .010 |
| | 145 | 4.14 | 33.31 | .009 |
| | 170 | 4.56 | 33.49 | .004 |
| | 200 | 5.83 | 34.08 | .005 |

GLADYS EDDY SEIWELL

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### Some Notes on the Ecological Requirements of the Amphipod, *Gammarus fasciatus*[1]

The importance of the fresh-water amphipod crustaceans as fish food has recently attracted considerable attention, particularly as regards their ecological requirements. The works of Titcomb[2] and of Pentland[3] should be mentioned in particular. Titcomb has pointed out that *Gammarus limnaeus* S. I. Smith is to be found only in waters which have a calcium (or magnesium) carbonate content of more than 200 parts per million *Gammarus fasciatus* Say on the other hand was found to tolerate waters where the calcium carbonate content was no more than from 3 to 5 parts per million. Pentland however states that the chemical composition of the water appears to have no effect upon the distribution of these crustaceans. The writer has recently pointed out[4] that complete intergradation of the morphological characters which distinguish *Gammarus limnaeus* and *G. fasciatus* occurs in certain areas. It is quite true that the nature of the ecological requirements of these scuds have not as yet been fully ascertained.

The following note bears upon the question of the ecological requirements of typical *Gammarus fasciatus*.

In connection with certain duties for the U. S. Bureau of Fisheries the writer examined a small stream called Elklick Creek in the vicinity of Parsons, Tucker County, West Virginia. This stream extends from a mountain top down to the Black River fork of the Cheat River, a distance of about three miles. Elklick Creek has several small tributaries but is fed mostly by two main branches at the extreme head. One of these has its origin in a spring from a limestone cave. The other branch is fed by water seeping through shale and sandstone. The water in these upper tributaries is shortly to be utilized for a public water supply for the city of Parsons by the construction of a dam. The engineer in charge of the project has made, accordingly, a rather thorough study of the water. The soap hardness, which in this instance is without much question the calcium carbonate content, is 27 parts per million in the cave spring branch. The chemical determinations were made at the chemical laboratories of the University of West Virginia. Below the place where the two tributaries join the soap hardness is 10 parts per million. This reduction in soap hardness is, of course, caused by dilution from the headwater tributary having its origin in the seepage springs passing through the shale and sandstone. The cave spring branch extends for only a trifle more than a quarter of a mile. The temperature of the water at the spring is 48° F. One hundred yards down stream the temperature had increased to 55° F. when the air temperature was 85° F. At the mouth of the Spring Branch the temperature was 61° F., the same as that of the tributary with the lower carbonate content. By far the greatest numbers of *Gammarus fasciatus* occurred in the vicinity of the spring where the temperature was coldest. Progressively down stream from the limestone cave spring these crustaceans became fewer and fewer in numbers until near the mouth only an occasional straggler was found. None at all occurred in the other tributary above or below the point where the cave spring branch entered.

These observations seem to indicate that temperature together with certain chemical requirements (carbonate content) play a part in the ecological distribution of these amphi-

[1] Published with the permission of the Commissioner of the United States Bureau of Fisheries.

[2] Titcomb, John W. 1928. The fresh-water shrimp for replenishing food in trout streams. *Trans. Amer. Fish. Soc. 1927*: 150–159; 1931. More about the fresh-water shrimp. *Trans. Amer. Fish. Soc. 1930*: 95–100.

[3] Pentland, Ernest S. 1931. Controlling factors in the distribution of *Gammarus. Trans. Amer. Fish. Soc. 1930*: 89–94.

[4] Creaser, E. P. 1934. The larger crustacea of the Raquette watershed. *Twenty-third Ann. Rep. New York Conser. Dept.* (supplement) 1933: 158–163.

pods. They prefer cold water and this fact should be considered in their economic utilization.

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## A SOIL SURFACE SAMPLER

In February 1934, a machine was devised for the purpose of driving insects from leaves, flowers, and other loose materials rapidly and quantitatively. There are numerous faults in methods used by ecologists in finding an accurate estimate of the arthropods of the forest or prairie floor, particularly the lack of accuracy in numbers and the length of time and labor involved. The Berlesi funnel is accurate and quantitative, but it is not an apparatus that can be used in the field. It has been modified in numerous ways by the application of heat which speeds up the process, but it still takes from eight hours to several days to drive forth the insects. Because of this, if a series of samples are collected, a whole battery of Berlesi funnels must be used and these are not very portable nor efficient in the field. Berlesi funnels modified by heat, covers, etc. are satisfactory for the laboratory.

Other methods used by ecologists, such as examining collections of leaves and dirt by hand, floating the insects out on water, killing all the animals by ether under a can of known area and examining the soil for them, or simply examining a given area of soil surface in the field, are inaccurate because minute arthropods escape notice and much time and energy are needed.

### DESCRIPTION OF THE APPARATUS

This soil surface sampler is designed to alleviate some of the faults of the Berlesi funnel and other methods. It consists of a tripod (fig. 1, *A*) made of three iron bars, simply ⅝″ reinforcing iron. This iron was cut into three legs 30″ long, each was pointed at one end and flattened, bent to an obtuse angle, and drilled at the other end with a ¼″ hole. This tripod supports horizontally a hand blower (*C*) from a blacksmith's forge. The blower is supported on the tripod by long ¼″ stove bolts put in place of shorter bolts that hold the two halves of the blower together. Two nuts are used on each bolt, one to hold the blower together, and the other to hold the leg in place. The bolt from a fourth hole is removed and two iron wires hooked in it. These wires support a blow torch (*B*) which is pointed into the opening of the blower through which the air is sucked. Considerable difficulty was experienced at first in finding a cheap, even, strong heat, but this is very satisfactory. The torch develops its own pressure and throws a hot even flame which, directed into the blower, heats the fan and the air passing into the blower as the crank is turned at a regular speed (about 35 revolutions a minute). Situated as they are, the gears of the blower do not become overheated and, although the oil melts away, they do not wear very rapidly. The advantage of the blow torch is that it will burn for more than an hour on a cup of gasoline. The torch itself, if properly cared for, will last nearly a year. The blower will not suck out the flame.

The hot blast of air leaves the blower and passes into a reducer (*D*) of galvanized sheet iron 8½″ long, which reduces the opening from 2½″ to ¾″. A long reducer is necessary or the air pressure blows back against the fan. This reducer fits over the nozzle of the blower and into the collar or galvanized metal nipple (*J*) on the end of the flexible metal tubing (*E*). This nipple is 2½″ long, soldered in the flexible tube, and, as it is one inch in diameter at the open end, fits over the reducer. The flexible tubing is 12″ long by 1″ in diameter. It is soldered to the end of the upper funnel (*F*). The two funnels (*F*) are of galvanized sheet iron 12″ in diameter and 12″ high. The upper funnel has the flexible tubing on the small end and a 1½″ collar at the wide end is crimped
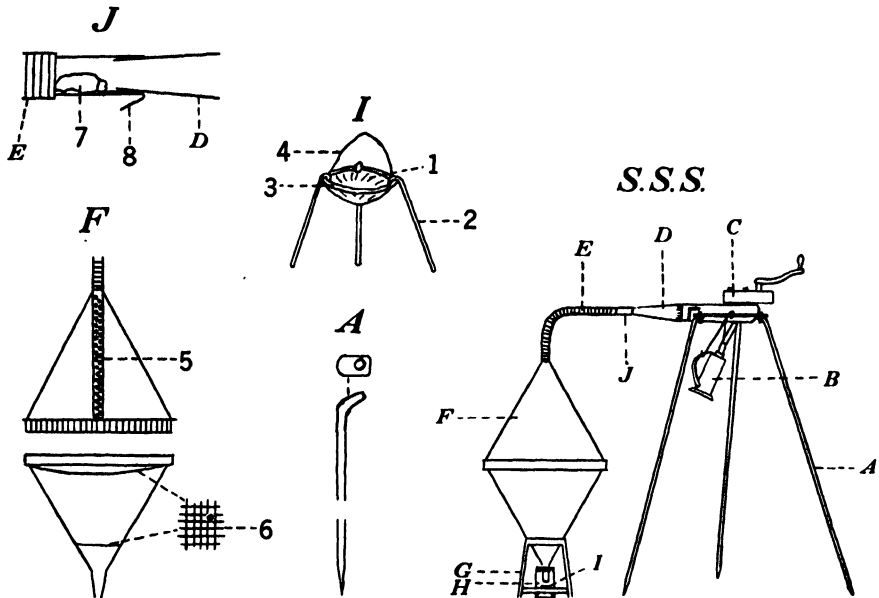
FIG. 1. Soil Surface Sampler, an apparatus for quickly driving insects from leaves, brush, flowers, and other loose materials.

**S.S.S.** The assembled apparatus.

*A.* Tripod made of three iron bars 30″ by ⅝″.

*B.* Heat applied from 98c, Montgomery-Ward and Co., blow torch. Supported by two iron wires.

*C.* Hand blower from a blacksmith's forge.

*D.* Reducer of galvanized metal, 8½″ long and reduces from 2½″ to ¾″.

*E.* Flexible metal tubing 12″ by 1″ with nipple of galvanized iron to fit over small end of reducer.

*F.* Two galvanized funnels 12″ in diameter and 12″ high with collar of upper one reduced to fit in collar of lower one. Collar 1½″.

*G.* Tripod of metal, bought at Montgomery-Ward and Co. 9″ High.

*H.* Pint mason jar with alcohol in bottom to catch insects as they leave the leaves.

*I.* Small tripod bearing sack to catch dirt that falls from funnels.

*J.* Galvanized nipple for fitting over end of reducer.

**A.** One leg of the large tripod showing the tip pointed and the upper end flattened and drilled with a ¼″ hole.

**F.** The two galvanized funnels.

    5. A 1″ metal tube 10″ long and perforated with numerous ⅛″ holes.

    6. Two hardware cloth rings with ½″ mesh. The upper one is loose and the lower one soldered in place.

**I.** Small tripod used in mason jar to catch debris.

    1. Screen sack.

    2. Iron wire legs, 2″ long.

    3. Iron wire ring to which screen is sewed, 1¾″ in diameter.

    4. Fine wire loop for picking tripod out of mason jar.

**J.** Nipple on flexible tubing.

    *E.* Flexible tubing.

    *D.* Reducer.

    7. Wad of cotton dipped in chemicals, the fumes of which drive out the insects.

    8. Fine wire to hold the cotton.

so that it will slip into a collar of the lower funnel. The lower funnel has the 1½" collar at the wide end and the small end is simply extended into a short tube. The upper funnel has a metal tube in it, 1" by 10", perforated with numerous ⅛" holes (*F*–5). The hot air passes from the flexible tubing into this and out through the holes. The lower funnel has near its base and soldered to it, a screen of ½" mesh hardware cloth (*F*–6). This screen is not really essential, but it serves to stop some of the debris that falls from the screen at the upper part of the funnel which is also ½" hardware cloth and is not attached.

The two funnels are supported by a tripod (*G*) 9" high. A pint mason jar (*H*) with alcohol in it is placed under the funnels. In the mason jar, standing in the alcohol, is a small tripod (*I*). This tripod is made of iron wire, the legs (*I*–2) being 2" long and the ring (*I*–1) 1¾" in diameter. A small net of screen (*I*–3) is sewed upon the ring and a handle of fine wire (*I*–4) is attached. This little tripod serves the very definite purpose of catching debris that falls from the funnels. The entire apparatus, materials and labor, cost about 15 dollars.

<center>USE OF THE APPARATUS</center>

One square foot samples of soil surface debris are taken at random in the habitats studied and immediately put in large No. 20 paper sacks with the proper labels. If working in the field, these are taken back to camp; if a laboratory is available they may be taken there and, if too wet may be allowed to dry a few hours by a radiator.

When ready to run the samples through the **S.S.S.** apparatus, it is assembled and the torch lighted, but not hung on the wires. The upper funnel is inverted and held between the knees with the end of the flexible tubing in a ½ pint tin can. This catches any debris. The sample is dumped into the funnel around the perforated tube and the screen and lower funnel quickly placed over it and forced on tightly. Then the funnels are turned over and the open end of the lower funnel placed in the can and the whole given a couple of shakes to knock the loose debris into it. The lid of the mason jar is quickly clapped over the can and the funnels placed on the tripod over the mason jar so that the descending arthropods will fall onto the screen net. The nipple of the flexible tubing is then forced over the reducer, the torch hung on the wires, and the blower started.

One of the faults which has not yet been overcome is the speed necessary in dumping the sample into the funnel and getting it covered. Lycosid spiders, flies, leafhoppers and others are so active that they may jump from the funnel before the lower one is placed over it.

The apparatus, now assembled, will drive out over 90 per cent of all arthropods in 15 to 30 minutes of steady cranking, depending upon the moisture in the sample. This is possible because of the large surface upon which the heat acts and through which the insects have to leave. As the apparatus becomes thoroughly heated those forms that are clinging to the sides of the lower funnel will let go and fall into the mason jar. As soon as they strike the screen they run around and fall off into the alcohol. If the sample is moist it takes longer to dry and the insects can stand great heat as long as it is moist. The majority of the forms dash from the apparatus in the first five minutes, but it takes another ten or fifteen minutes to drive them all out. When the sample is free of insects (5 minutes after last has dropped), the leaves may be dumped out and the tripod taken from the mason jar. The debris that is in the screen is sifted on a fine screen over the mason jar and all mites will fall into the alcohol. Other insects may be picked out. The debris in the tin can is then looked through and, as it is always small, all arthropods can be captured in a minute or two.

A further step toward speeding up the process of removing the insects is shown in **J**. A wad of cotton (*J*–7), attached to a fine wire (*J*–8), is dipped into creosote or cresylic acid and placed in the nipple (*J*) when the flexible tube is connected to the reducer. In this way, the hot air, passing over the chemical, carries the fumes into the funnels and

NOTES AND COMMENT

drives out the insects. Creosote is very effective in driving out collembola, chinch bugs, beetles, etc., but is not so effective in driving out spiders and ants. This field has not been explored very extensively and some material may be found the hot fumes of which are very repellent to all forms. It must not be too repellent to the observer.

## DISCUSSION AND CRITICISM

This apparatus has now been used with success for nearly a year. More than 30,000 arthropods have been driven out of 210 square feet of soil surface materials, which is an average of 140 specimens per square foot. No sample has been free of arthropods and the highest taken for one square foot has been 4000. The great majority of forms on the floor have been collembola and mites which readily come through.

As a method of checking the accuracy of the S.S.S., at different times, samples were examined for insects dead or alive after being subjected to heat. Only when the apparatus was first built and different fuels were being used were any forms killed by fumes or heat. The gasoline heat does not kill. Ten samples examined during the fall showed a total of 148 insects still present after being heated, while 1434 were driven out. This is 90 per cent of the total. The error for the entire work is not more than 10 per cent and this may be considered low compared to other quantitative methods. When pressed for time, 20 or 30 samples may be run through the apparatus in a day.

In criticism of the S.S.S. apparatus, it appears to have two major faults; it is not quite accurate enough, a 98 per cent perfect record being desired, and it is still not fast enough for wet samples. It is bulky and heavy, but can be completely dismantled and is then portable. The samples still have to be handled too much and some specimens are lost in handling. It has to be watched, but if used in the laboratory, electric hairdriers may take the place of the blower and torch or an electric mixer can be used to turn the blower by a belt fixed on a pulley on the crank's shaft.

## SUMMARY

An apparatus, the soil surface sampler, for driving arthropods from soil surface debris, flowers and other loose materials is figured and described.

This machine has been in use for a year and is at least 90 per cent perfect in driving all the arthropods from one square foot samples of soil debris.

Over 30,000 arthropods have been driven from 210 square feet of material.

The machine can be built for $15.00 or less and overcomes many faults in methods used by many ecologists.

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